University of Alberta

The impacts of variable retention harvesting on spruce beetle (*Dendroctonus rufipennis*) and canopy dwelling Lepidopteran parasitoids in the boreal forest.

by

Julia Wesley

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **Master of Science**

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Fall 2002

National Library of Canada
Acquisitions and Bibliographic Services
395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada
Acquisitions et services bibliographiques
395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-81497-1

Canada

University of Alberta

Library Release Form

Name of Author: Julia Wesley

Title of Thesis: The impacts of variable retention harvesting on spruce beetle (*Dendroctonus rufipennis*) and canopy dwelling Lepidoptera parasitoids in the boreal forest.

Degree: Master of Science

Year this Degree Granted: 2002

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly, or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

Julie Wesley

#127, 5166 Halifax Street
Burnaby, British Columbia
Canada, V5B 2N6

Date: Apt. 23/02

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis **The impacts of variable retention harvesting on spruce beetle (D*endroctonus rufipennis*) and canopy dwelling Lepidoptera parasitoids in the boreal forest** submitted by **Julia Wesley** in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

Dr. John. R. Spence

Dr. David W. Langor

Dr. Fiona K.A. Schmiegelow

Dr. Felix A.H. Sperling

Date: Sept 23. 02

Abstract

This research is a component of the EMEND (Ecosystem Management Emulating Natural Disturbance) project in northwestern Alberta, that aims to explore the feasibility of aspects of Natural Disturbance Paradigm as an approach to forest management. I studied parasitoids of canopy-dwelling larval Lepidoptera on spruce and aspen and parasitoids of *Dendroctonus rufipennis* (Kirby). The defoliator parasitoids were studied pre- (1998) and post-treatment (1999). Conifer dominated stands had significantly more diverse parasitoid communities compared to deciduous stands and deciduous stands with a spruce understory. Also, parasitoids were significantly more abundant during spring than early summer. Rarefaction curves suggest conifer-dominated control stands had higher parasitoid diversity than conifer-dominated 50% residual stands. *Dendroctonus rufipennis* supported 4 parasitoid species that was compared among 20%, 50% residual and uncut control compartments. Parasitoids had preferential sites for oviposition and were abundant in different treatments. There was a significant inverse relationship between available beetle density and percent parasitism.

Acknowledgements

First, I thank my family for support during this degree; they have always supported me and my decisions. I am especially grateful for all of the love, patience and unwavering support that my husband, Paul Wesley, has demonstrated throughout my degree. Second, I would like to thank my supervisors John Spence and Dave Langor for their time and input during my thesis. John Spence supported my learning experiences including many conferences and a hymenopteran identification trip to Ottawa while Dave Langor coached me through some difficult thesis synthesis with encouragement. For parasitoid identification, I thank taxonomists at the Canadian National Collection in Ottawa, Ontario– Henri Goulet, Gary Gibson, and John Huber. Field and laboratory assistance for this project was provided for by a number of cheerful and helpful people. These include Gayle Caltagirone, Michelle Dias, Carmen Gibbs, Louis Morneau, Sam Price and the 1998 - 1999 EMEND core crew. In addition, a vast array of help was received from Northern Forestry Center and University of Alberta staff including Daryl Williams, Greg Pohl, Jim Hammond, Colin Myrholm, Jan Volney, Ken Mallett, Jon Elofson, and Karen Cryer.

Financial assistance was provided by Sustainable Forest Management Network of the NCE, Daishowa- Marubeni International Ltd., Canadian Forest Products Ltd., Manning Diversified Forest Products Research Trust Fund,

Biodiversity Grants Program (Biological Sciences, University of Alberta), and Canadian Circumpolar Institute- BAR Grant.

Table of Contents

Chapter 1. Introduction 1

1.1 Evolution of forest management policy. 1

1.2 The EMEND experiment. 2

1.3 Biodiversity as a response parameter. 4

1.4 Study taxa 5

1.5 Thesis objectives. 6

1.6 References. 9

Chapter 2. Structure of parasitoid assemblages of mixedwood defoliators: and initial responses to variable retention harvesting. 16

2.1 Synopsis 16

2.2 Introduction 17

2.3 Methods and Materials 19

2.3.1 Site and General Experimental Context 19

2.3.2 Defoliator and Parasitoid Sampling 20

2.3.3 Defoliator and Parasitoid Rearing 22

2.3.4 Statistical Analysis 24

2.4 Results 26

2.4.1 Parasitoid-host associations and assemblage structure . 26

2.4.2 Temporal Variation. 28

2.4.3 Spatial Variation 30

I) *Cover Type* 30

II) *Aspen versus spruce* 32

III) *Harvesting Treatment* 32

2.5 Discussion 35

2.6 References 40

Chapter 3. The impacts of variable retention harvesting on spruce beetle (*Dendroctonus rufipennis*) parasitoids. 57

3.1 Synopsis 57

3.2 Introduction 58

3.3 Methods and Materials 61

3.3.1 Study Site 61

3.3.2 Sampling of spruce beetle and parasitoids 62

3.3.3 Parasitoid Rearing and Identification 64

3.3.4 Calculation of percent parasitism and development index 65

3.3.5 Emergence, flight and behavior 66

3.3.6 Statistical Analysis 68

3.4 Results 69

3.4.1 *D. rufipennis* Development 69

3.4.2 Parasitoid Assemblage Structure 71

3.4.3 Treatment effects on parasitism 73

3.4.4 Parasitoid Phenology and Behavior 75

3.5 Discussion 77

3.5.1 *Spruce beetle development and host availability* 77

3.5.2 *Parasitoid assemblage structure and biology* 79

3.5.3 *Parasitoid responses to treatments.* 83

3.6 References 87

Chapter 4. Discussion 107

4.1 Lepidopteran Parasitism. 107

4.2 *Dendroctonus rufipennis* parasitism. 109

4.3 Future Directions. 111

4.4 References. 114

Appendix 1. Recipe for rearing medium for parasitoids of *Picea glauca* bud defoliators and *Dendroctonus rufipennis*.. 119

Appendix 2. Cephalic morphology of larvae of parasitoids of the spruce beetle and a key to species. 121

2.1. Introduction. 121

2.2. Methods. 122

2.3. Results. 123

2.4. Parasitoid Description. 124

2.5. References. 127

List of Tables

Table 2.1. Number of aspen and spruce trees sampled in each treatment pre - (1998) and post - (1999) harvest and stand type used in analysis. ... 47

Table 2.2. Lepidoptera and sawfly hosts reared from aspen and spruce in 1998 and 1999. Stand abbreviations are: DD- deciduous dominated; CD- conifer dominated; and DU-A and DU-S are aspen and spruce respectively sampled from deciduous dominated with spruce understory. 48

Table 2.3. Parasitoids reared from Lepidoptera and Symphyta defoliators of spruce and aspen in 1998 and 1999. 49

Table 2.4. Summary of lepidopteran hosts and parasitoid abundance, species richness and species diversity from samples collected in AD, CD, and DU cover types from a) spruce, b) aspen and c) post-treatment aspen and spruce. Comparisons with the different letters denote statistical significance. 52

Table 3.1. Average development index (± SE) of *Dendroctonus rufipennis* in: a) harvesting treatments and; b) different log surfaces in 1999. In columns with significant main effects as determined by ANOVA (α=0.05), cells with the same letter indicate no significant difference (Bonferroni tests). 97

Table 3.2. Numbers (%) of spruce beetle progeny attacked by each of four parasitoid species for each log surface.. 98

Table 3.3. Number of 100 cm^2 bark samples containing available *D. rufipennis* hosts discovered by parasitoids in each a) treatment and b) log surface 99

Table 3.4. Mean parasitism proportion (± SE) for available beetles contained in discovered log samples in each a) treatment ($F_{3, 31}$= 0.667, P = 0.581) and b) log surface ($F_{3, 31}$ = 0.727, P = 0.546). Beetle density was used as a covariate in this Univariate GLM ($F_{1, 33}$ = 22.202, P < 0.001). . 100

Table 3.5. Numbers (%) of spruce beetle progeny attacked by each of four parasitoid species. 101

Table 3.6. Number of parasitoid larvae and cocoons collected and reared from all 100 cm^2 bark samples in treatments and controls for 4 sample dates. 102

List of Figures

Figure 2.1. Rarefaction curves for Lepidoptera and parasitic Hymenoptera species collected from *P. glauca* trees felled in CD and DU stands. Comparisons were made between A) 1998 and 1999 CD and DU Lepidoptera and B) parasitoids reared; C) combined early and late 1998 and 1999 Lepidoptera and D) parasitoids reared CD and DU control locations. 54

Figure 2.2. Rarefaction curves for Lepidoptera and parasitic Hymenoptera species collected from *P. glauca* trees felled in CD and DU stands. Comparisons were made between A) early 1998 Lepidoptera and B) parasitoids reared from CD and DU stands; C) 1999 Lepidoptera and D) parasitoids reared CD stands.. 55

Figure 2.3. Rarefaction curves for Lepidoptera and parasitic Hymenoptera species collected from post- treatment *P. tremuloides* trees felled in DD and DU stands. Comparisons were made between A) Lepidoptera and B) parasitoids reared from DD and DU stands; C) Lepidoptera and D) parasitoids reared from DD 20% and 50% residual treatments and DU control locations. 56

Figure 3.1. Comparisons of means (± SE) density (per 100 cm^2) of: a) available hosts and; b) percent parasitism of available hosts for each treatment and log surface. Data represent all 144 bark samples collected on August 17, 1999. 103

Figure 3.2. Percent of parasitoid larvae in samples collected from July 19, 1999 to July 21, 2000 represented by different species, partitioned by: a)

harvesting treatment; and b) log surface. Number of parasitoid individuals is indicated at the top of each bar. 104

Figure 3.3. Comparisons of means (± SE) % parasitism per sample containing available beetle hosts, total number of parasitised hosts, and total of available hosts for a) clear-cut, b) 20% residual, c) 50% residual, and d) control compartments..... 105

Figure 3.4. Flight activities for parasitoids based on combined observations of specimens on logs and in lindgren, emergence and sticky traps and number of parasitoids present in 144 bark samples for each date (all treatment and log surfaces combined) for a) *Coeloides rufovariegatus*, b) *Bracon tenuis*, c) *Roptrocerus rufovariegatus*, and d) *Dinotiscus dendroctoni*. 106

Chapter 1

INTRODUCTION

1.1 EVOLUTION OF FOREST MANAGEMENT PHILOSOPHY

The forest industry is economically important to Canada. For example, in 2000, it contributed $20.8 billion to the Canadian Gross National Product and directly employed 373,326 people (Natural Resources Canada 2001). The 1992 United Nations Conference on Environment and Development, as well as subsequent international and national increases in large-scale harvesting of the world's forests, has raised public concern about sustainability of forested ecosystems (Pratt and Urquhart 1994). In response, the past view that forests were to be managed for fiber and a few organisms of economic or recreational value (Society of American Foresters 1991) is evolving toward a broader ecosystem-based philosophy of management (Andreasen *et al.* 2001, Kimmins 1995, Kurtz *et al.* 2001), although mechanisms and trade-offs in implementing this shift in paradigm inspires considerable debate.

Historically, natural disturbances, such as wildfire, blowdown, insect outbreaks and fungal attacks, have shaped forest ecosystems in boreal forests (Bonan and Shugart 1989). Recent approaches to sustainable forestry and ecosystem preservation call for emulation of natural disturbances, especially wildfire, and maintenance of natural pathways for forest succession (Holdgate

1996; Hunter 1993; Society of American Foresters 1991), this philosophy is often designated the Natural Disturbance Paradigm (NDP). Among other assumptions, this model suggests that forest growth can be balanced with natural depletion to allow foresters to plan long-term production goals while maintaining ecosystem components (Hunter 1993). As wildfire is usually held to be the principal agent of natural disturbance in boreal forests, it is argued that forestry practices, within the context of the NDP, must attempt to emulate key structural and functional features relevant to wildfire (Angelstam 1998; DeLong and Tanner 1996) to maintain biota adapted to wildfire succession (Holliday 1992, Muona and Rutanen 1994).

1.2 THE EMEND EXPERIMENT

The EMEND (Ecosystem Management Emulating Natural Disturbance) Project, is an extensive, long term, multidisciplinary forest management experiment that aims to explore the feasibility of aspects of NDP as an approach to forest management (Jamieson, 2001b). Located 85 km northwest of Peace River (Alberta), the experiment and its buffers, roads and landings comprise about 1500 ha of a currently managed forestry land base in the boreal mixedwood plains forest (Jamieson 2001a). The objectives of EMEND are: 1) to determine which forest harvest and regenerative practices best maintain biodiversity, forest structure and functional ecosystem integrity in

comparison to forest landscapes originating via natural disturbances; and 2) to explore trade-offs among environmental, economic and sociological values.

Four cover types were chosen along the typical successional continuum in boreal mixedwoods: 1) Deciduous dominated (DD) - greater than 70% of canopy trees as trembling aspen, *Populus tremuloides* Michx. or balsam poplar, *Populus balsamifera* L.; 2) Deciduous dominated with spruce understory (DU) - as in DD but with understory of white spruce, *Picea glauca* (Moench) Voss, at least 30% as tall as dominant trees; 3) Mixed (MX) - both hardwood and softwood components comprising 40-50% of the canopy trees in the stand; and 4) Conifer dominated (CD), greater than 70% of canopy trees as *P. glauca* (Spence and Volney 1999). Five harvesting treatments were applied to ~10-ha compartments that left 2% (clear-cut), 10%, 20%, 50% or 75% residual live standing trees in compartments as well as uncut controls. Residual treatments were achieved with 5-meter wide machine corridors to allow individual tree removal within 15-meter wide retention strips (Sidders and Spence 1999). All treatments in the above cover classes were replicated three times and harvesting was completed during the winter of 1998-99. Additional compartments were burned or scheduled for whole-compartment burns and others are scheduled for harvest and slash-burn treatments. Given the demands of my study relative to resources available, I was able to use only a subset of the treatment options for my research.

1.3 BIODIVERSITY AS A RESPONSE PARAMETER

The central question of the EMEND experiment and my work is: How much residual is enough to preserve and protect critical aspects of ecosystem function? Ecosystem integrity and function are difficult to measure directly so biodiversity parameters are typically chosen as surrogate indicators (Noss 1995) in recognition that heterogeneity at different ecological levels is a fundamental property of natural systems (Haila and Kouki 1994). Biodiversity encompasses total heredity variation in life forms across all levels of biological organization from genes to entire ecological communities (Wilson 1994).

Global biodiversity cannot be practically measured and we do not even know the number of species to the nearest order of magnitude (Wilson 1985). Therefore, biological indicators are appointed and measured in proxy. McGeoch (1998) suggested criteria for selecting taxa to indicate environmental, ecological, or biodiversity change.

In the last three decades, concerns about rapidly accelerating loss of biodiversity has been raised by biologists, foresters and the general public (Silbaugh and Betters 1995). Conservation of our biota is now considered an important and necessary part of resource management (Probst and Crow 1991, Burton *et al.* 1992). Since invertebrates represent over 80% of the world's described species (Wilson 1992) and perform numerous vital roles in forest ecosystems, we seek to understand how harvesting affects these invertebrate communities.

1.4 STUDY TAXA

Insects are ideal study organisms to serve as biological indicators of ecosystem perturbation and recovery as they are readily surveyed, sensitive to environmental disturbance (Pearson 1994), taxonomically and trophically diverse, easily collected, and perform critical ecological processes (Grove 2001, Mattson and Addy 1975, McGeoch 1988, New 1995, Seastedt and Crossley 1984). Although relatively little is known about these small organisms compared to the more charismatic mega-fauna and flora, insects comprise the vast majority of biological diversity in all terrestrial ecosystems (Golley 1977). In forests, insects are central to many ecosystem functions (Wilson, 1992; British Columbia Ministry of Forests and Lands 1987; Mattson and Addy 1975) but large populations of defoliators and wood boring insects can significantly reduce fiber production (Coulson and Witter 1984).

Fortunately, many insect populations are partly regulated by parasitoids, and density-dependant host-parasitoid relationships are thought to contribute to overall system stability (Hassell 1986; LaSalle 1993; LaSalle and Gauld 1993). Female parasitoids oviposit on or near a suitable host that the larva consumes to complete its own development (Waage and Greathead 1986). However, due to their high trophic position, parasitic Hymenoptera are very sensitive to environmental disturbance (Kreuss and Tscharntke 2000; LaSalle 1993). Reduced parasitoid populations may allow pest populations to outbreak,

resulting in lowered forest production and conflict with sustainability goals. These relationships, although important aspects of ecosystem function (Bouletreau 1986), are frequently ignored in forest planning. Host-parasitoid linkages are poorly understood in northern forest ecosystems (May 1988), but conserving these relationships is essential to ensure that forestry activities do not compromise natural regulation of potential pest populations.

Parasitic Hymenoptera are one of the largest groups of insects with more than 100,000 species estimated to occur worldwide (Gauld and Bolton 1988; Wahl and Sharkey 1993) with an apparently greater diversity in temperate locations rather than tropics (Owen and Owen 1974). LaSalle and Gauld (1992) suggest that 70% of these insects have yet to be even described and thus their importance is poorly understood. Relatively little is known about host specificity and behavior for most species, and about community structure of parasitoids (Askew and Shaw 1986; Memmott *et al.* 1994). Therefore, it is necessary to collect basic biological information in addition to ecological information. The taxonomic challenges inherent in working with parasitic wasps exclude them from many studies of biodiversity.

1.5 THESIS OBJECTIVES

I have investigated relationships between parasitoids and two types of phytophagous forest insects, defoliators that reduce tree fiber production (Natural Resources Canada 1998), and spruce beetles that kill valuable trees

(DeLeon 1935; Massey 1961). My research objectives were 1) to establish host-parasitoid associations by rearing parasitised hosts, 2) to develop a better understanding of how parasitoids may regulate potential forest pest species in the northern boreal forest, 3) and to assess impacts of forest harvesting on host-parasitoid relationships. This research provides the first community level study of host-parasitoid relationships in the western boreal forest of North America. My results contribute to assessing biodiversity and to better understanding critical ecosystem processes that regulate insect outbreaks.

Chapter two focuses on the parasitoid community of canopy-dwelling Lepidoptera to identify host-parasitoid relationships; measure species richness, abundance and diversity of the parasitoids; and estimate percent parasitism. These elements were compared across treatment (20 and 50% residual, control), cover type (DD, DU, CD), and tree species (*P. tremuloides* and *P. glauca*). Structure and diversity of parasitoid complexes (Lewis and Whitfield 1999, Kreuss and Tscharntke 2000), are altered by forest harvesting. Parasitic hymenopterans are commonly more sensitive to disturbance than their phytophagous hosts (LaSalle 1993) and this could have serious implications for regulation of defoliator populations on forested land bases subjected to large-scale industrial forestry.

Chapter three addresses parasitism of the spruce beetle, *D. rufipennis*. Parasitoids were identified and percent parasitism was measured in the aftermath of variable retention harvest. Parasitism and beetle development was

compared across treatments (clear cut, 20 and 50% residual, control), and sample locations on the sample bolt (top, sides, bottom) in CD compartments. The spruce beetle is one of the most destructive pests of mature spruce in North America (Humphreys and Safranyik 1993, Schmid and Frye 1977, Werner *et al.* 1977). After harvesting, beetle populations can build up in fresh downed woody material and often precipitate into outbreaks in surrounding forest (Reynolds and Holsten 1994; Wygant and Lejeune 1967). Parasitoids have the ability to regulate insect populations to reduce outbreak potential (Dahlsten 1982; DeLeon 1935; Linit and Stephen 1983; Moore 1972). However, the impact of parasitoids on endemic *D. rufipennis* populations and their role in *D. rufipennis* epidemiology is largely unknown (Moeck and Safranyik 1984).

Chapter four summarizes, discusses and integrates results from chapters 2 and 3. These results are placed into a management perspective and the most important messages are emphasized.

1.6 REFERENCES

Andreasen, J.K., R.V.O. O'Neill, R. Noss, and N. C. Slosser. 2001. Considerations for the development of a terrestrial index of ecological integrity. *Ecological Indicators.* I: 21-35

Angelstam, P. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sci.* **9:** 593-602.

Askew, R.R. and M.R. Shaw. 1986. Parasitoid communities: their size, structure, and development. *In:* Insect Parasitoids. (K. Waage and D. Greathead, Eds.), pp. 225-264. Academic Press, London.

Bonan, G.B. and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. *Ann. Rev. Ecol. Sys.* **20:** 1-28.

Bouletreau, M. 1986. The genetic and co- evolutionary interactions between parasitoids and their hosts. *In*: Insect parasitoids (Waage, J. and D. Greathead, Eds.), Academic Press, London, pp. 169-200.

British Columbia Ministry of Forests and Lands. 1987. Bark Beetles- A threat to our forests. Queen's Printer for British Columbia.

Burton, P.J. A.C. Balisky, L.P. Coward, S.G. Cumming, and D.D. Kneeshaw. 1992. The value of managing for biodiversity. *For. Chron.* **68**: 225-237.

Coulson, R.N., and J.A. Witter. 1984. Forest Entomology: ecology and management. Wiley, New York.

Dahlsten, D.L. 1982. Relationships between bark beetles and their natural enemies. Pp. 140-182 In: Bark Beetles in North America Conifers, (J.B. Mitton and K.B. Sturgeon, Eds.). Univ. of Texas, Austin.

DeLeon, D. 1935. The biology of *Coeloides dendroctoni* Cushman (Hymenoptera- Braconidae) an important parasite of the Mountain Pine beetle (*Dendroctonus monticolae* Hopk.). *Ann. Ent. Soc. Am.* **28**(4): 411-424.

DeLong, S.C. and D. tanner. 1996. Managing the pattern of forest harvest: lessons from wildfire. *Biodiversity and Conserv.* **5:** 1191- 1205.

Gauld, I.D., and B. Bolton. 1988. The Hymenoptera. British Museum (Natural History) and Oxford University Press, Oxford.

Golley, F.B. 1977. Insects as regulators of forest nutrient cycling. *Trop. Ecol.* **18**: 116-123.

Grove, S.J. 2001. Tree basal area and dead wood fauna as surrogate indicators of saproxylic faunal integrity: a case study from the Australian lowland tropics. *Ecological Indicators.* **1**: 171-188.

Haila, Y. and J. Kouki. 1994. The phenomenon of biodiversity in conservation biology. *Ann. Zool. Fenn.* **31:** 5-18.

Hassell, M.P. 1986. Parasitoids and population regulation. *In:* Insect Parasitoids (Waage, J. and D. Greathead, Eds.), Academic Press, London, pp. 201-224.

Holdgate, M. 1996. The ecological significance of biological diversity. *Ambio.* **25(6);** 409-416.

Holliday, N.J. 1992. The carabid fauna (Coleoptera: Carabidae) during post-fire regeneration of boreal forest: properties and dynamics of species assemblages. *Can J. Zool.* **70:** 440- 452.

Hunter, M.L. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biol. Conserv.* **65:** 115- 120.

Humphreys, N. and L. Safranyik. 1993. Spruce Beetle. Canada- B.C. Partnership Agreement FRDA II: For. Pest Leaf. 13. 7pp.

Jamieson, S. 2001a. Making EMENDS. *Can. Forest Industries.* **Nov./ Dec.** p. 14-20.

Jamieson, S. 2001b. We are that good. *Can. Forest Industries.* **Nov./ Dec.** p. 6.

Kimmins, J.P. 1995. Sustainable development in Canadian forestry in the face of changing paradigms. *For. Chron.* **71**(1): 33-40.

Kruess, A. and T. Tscharntke. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicea sepium*. *Oecologia.* **122**: 129- 137.

Kurtz, J.C., L.E. Jackson, and W.S. Fisher. 2001. Strategies for evaluating indicators based on guidelines from the Environmental Protection Agency's Office of Research and Development. *Ecological Indicators.* **1**: 49-60.

LaSalle, J. 1993. Parasitic Hymenoptera, Biological Control and Biodiversity. *In*: Hymenoptera and Biodiversity (LaSalle, J. and I.D. Gauld, Eds.), CAB International, Wallingford, pp. 197-215.

LaSalle J. and I.D. Gauld. 1992. Parasitic Hymenoptera and the biodiversity crisis. *Redia* **74**: 315- 334.

LaSalle, J. and I.D. Gauld. 1993. Hymenoptera: Their Diversity and Their Impact on the Diversity of Other Organisms. *In*: Hymenoptera and Biodiversity (LaSalle, J., and I.D. Gauld, Eds.), CAB International, Wallingford, pp. 1-26.

Lewis, C.N. and J.B. Whitfield. 1999. Braconid wasp (Hymenoptera: Braconidae) diversity in forest plots under different silvicultural methods. *Community and Ecosystem Ecol.* **28** (6): 986- 993.

Linit, M.J. and F.M. Stephen. 1983. Parasite and predator component of within-tree southern pine beetle (Coleoptera: Scolytidae) mortality. *Can. Entomol.* **115**: 679-688.

Massey, C.L. 1961. Biology of the Southwestern Pine Beetle, *Dendroctonus barbari*. *Ann. Entomol. Soc. Am.* **54**:354- 359.

Mattson, W.J. and N.D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science*. **190**(4214): 515-522.

May, R.M. 1998. How many species are there on Earth? *Science*. **241**: 1441-1449.

McGeoch, M.A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biol. Rev.* **73:** 181- 201.

Memmott, J., H.C.J. Godfray and I. D. Gauld. 1994. The structure of a tropical host- parasitoid community. *J. Anim. Ecol.* **63**: 521- 540.

Moeck, H.A. and L. Safranyik. 1984. Assessment of predator and parasitoid control of bark beetles. Pacific For. Res. Center. Inf. Rep. BC- X- 248.

Moore, G.E. 1972. Southern pine beetle mortality in North Carolina caused by parasites and predators. *Env. Entomol.* **1**(1): 58-65.

Muona, J. and I. Rutanen. 1994. The short- term impact of fire on the beetle fauna in boreal coniferous forest. *Ann. Zoologici Fennici.* **31:** 109- 121.

Natural Resources Canada. 2001. The State of Canada's Forests 2000-2001. *Natural Resources Canada, Canadian Forest Service*, Ottawa, Ont.

New, T.R. 1995. Introduction to invertebrate conservation biology. Oxford University Press, Oxford, U.K. 194pp.

Noss, R. 1995. Maintaining ecological integrity in representative reserve networks. *World Wildlife Fund.*

Owen, D.F. and J. Owen. 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature.* **249**: 583- 584.

Pearson, D.L. 1994. Selecting indicator taxa for the quantitative assessment of biodiversity. *In*: Philosophical Transactions: Biological Sciences (D.L. Hawksworth, Ed.), Royal Society, London, pp. 75-79.

Pratt, L. and I.T. Urquhart. 1994. The last great forest: Japanese multinationals and Alberta's northern forests. NeWest Publishers Limited, Edmonton.

Probst, J.R. and T.R. Crow. 1991. Integrating biological diversity and resource management. *J. For. Chron.* **89**: 12-17.

Reynolds, K.M. and E.H. Holsten. 1994. Relative importance of risk factors for spruce beetle outbreaks. *Can. J. For. Entomol.* **24**: 2089 -2095.

Schmid, J.M. and R.H. Frye. 1977. Spruce beetle in the Rockies. USDA Forest Service, Rocky Mountain Forest and Range Experimental Station. Gen. Tech. Rept. RM-49, 38 pp.

Seastedt, T.R. and Crossley Jr., D.A. 1984. The influence of arthropods on ecosystems. Bioscience 34(3): 157-161.

Silbaugh J.M. and D.R. Betters. 1995. Quantitative biodiversity measures applied to forest management. *Envlron. Rev.* **3**: 277-285.

Society of American Foresters. 1991. Task force report of biological diversity in forest ecosystems. Soc. Am. Foresters, Bethsda, MD.

Spence J.R., and W.J.A. Volney. 1999. EMEND: ecosystem management emulating natural disturbance. *SFMN Proj. Rept.* 17pp.

Sidders, D. and J.R. Spence. 1999. Ecosystem Management Emulating Natural Disturbance: Research study and field guide.

Waage, J. and D. Greathead. 1986. Preface. *In*: Insect parasitoids (Waage, J. and D. Greathead, Eds.), Academic Press, London, pp. xi-xii.

Wahl, D.B. and M. Sharkey. 1993. Superfamily Ichneumonoidea. Hymenoptera of the World: An identification guide to families (H. Goulet and J.T. Huber, Eds.), Canada Communications Group, Ottawa, Canada.

Werner, R.A., B.H. Baker and P.A. Push. 1977. The spruce beetle in white spruce forests of Alaska. U.S.D.A For. Serv. Gen. Tech. Rept. PNW-61. 13pp.

Wilson, E.O. 1985. The biological diversity crisis: a challenge to science. *Issues in Sci. and Tech.* **2:** 20- 29.

Wilson, E.O. 1992. The diversity of life. W.W. Norton and Company, New York. 424 p.

Wilson, E.O. 1994. Naturalist. Island Press, Washington, D.C.

Wygant, N.D. and R.R. Lejeune. 1967. Engelmann spruce beetle *Dendroctonus obesus* (Mann.). *In*: Important Forest Insects and diseases of mutual concern to Canada, the United States and Mexico. Canada Dept. For. Rural Development Publ. 1180.

Chapter 2

STRUCTURE OF PARASITOID ASSEMBLAGES OF MIXEDWOOD DEFOLIATORS: AND INITIAL RESPONSES TO VARIABLE RETENTION HARVESTING.

2.1 SYNOPSIS

Parasitoids were reared from lepidopteran caterpillars collected on *Populus tremuloides* or *Picea glauca* in Northwestern Alberta using whole tree sampling, both pre-harvest (1998) and one season after variable retention harvests (1999). Analysis of Variance (General Linear Model) were used to compare parasitoid abundance, parasitoid richness, defoliator abundance, defoliator richness and lepidopteran parasitism among harvesting treatments (20, 50% residual and uncut control compartments) and forest cover types (deciduous dominated, deciduous with a spruce understory and conifer dominated). The parasitoid community differed significantly among forest cover types. Conifer dominated stands had the most diverse parasitoid assemblage and parasitoids were significantly more abundant during spring than early summer. Initial effects of variable retention harvesting treatments on parasitoid assemblages could not be demonstrated by ANOVA but rarefaction curves suggest that CD control stands had higher parasitoid diversity than CD 50% residual stands.

2.2 INTRODUCTION

Structure and diversity of arthropod assemblages (e.g. Buddle *et al.* 2000, Huhta 1971, Niemela *et al.* 1993, Paquin and Coderre 1997, Szujecki 1972), including parasitoid complexes (Lewis and Whitfield 1999, Kreuss and Tscharntke 2000), are altered by forest harvesting. Differences in microclimatic conditions, increased susceptibility to predation, and reduced movement between fragmented patches have been suggested as explanations for these changes (Powell and Powell 1987, Zuidema *et al.* 1996).

Parasitic Hymenoptera are generally more sensitive to disturbance than their phytophagous hosts. Thus, local populations of parasitoids may be more vulnerable to extirpation than those of their hosts (LaSalle 1993, Kruess and Tscharntke 2000) and this could have serious implications for regulation of defoliator populations on forested land bases subjected to large-scale industrial forestry. Organisms like parasitoids that operate at higher trophic levels may be effective regulators even at low population sizes, and thus are more sensitive to extirpation following disturbance (LaSalle and Gauld 1992). Furthermore, their sensitivities to habitat structure, potential importance in regulating pest population dynamics and the fact that parasitic Hymenoptera are highly specialized, suggest that they should be excellent and sensitive indicators for general environmental features (Lewis and Whitfield 1999). Therefore, understanding parasitoid response to new harvesting techniques is important

on at least two accounts, both as indicators of environmental conditions and as natural regulators of potential pest populations.

Through their regulatory influences, some parasitoids may be "keystone species" so that their removal could cause a cascade of effects leading to significantly altered biological communities and ecosystems (LaSalle 1993, Memmott and Godfray 1993). Most importantly, from a pure biodiversity perspective, the parasitic Hymenoptera comprise a large number of poorly known species, and their detailed trophic involvement in communities provides a strong force structuring the diversity of other organisms (LaSalle and Gauld 1992). Thus, both as potential indicators connected to ecosystem function and as biologically diverse faunal elements, parasitoid assemblages demand our attention in thorough biodiversity studies.

This chapter focuses on the biodiversity of parasitoids utilizing hosts feeding in the canopy of a boreal forest. Unlike other insects, the known diversity of parasitic Hymenoptera is greater in temperate zones than in the tropics (Janzen 1981; Janzen and Pond 1975; Owen and Owen 1974). This is perhaps because most tropical parasitic Hymenoptera have yet to be described (LaSalle and Gauld 1992) and understood biologically (LaSalle and Gauld 1993), but clearly their high numbers in temperate and boreal regions underscore potentially important ecological implications of their diversity. In this chapter, I provide new information about parasitoid assemblages from the western Canadian mixedwood region and their response to logging.

Furthermore, I contribute data about poorly known defoliator host-parasitoid relationships and provide a basis for predictions about parasitoid abundance, richness, diversity, and parasitism for the boreal mixedwood. Specifically, I asked whether parasitism and the structure of parasitoid assemblages were affected by forest cover type or by several levels of retention harvest.

2.3 MATERIAL AND METHODS

2.3.1 Site and General Experimental Context

This work was conducted on the site of the EMEND (Ecosystem Management Emulating Natural Disturbance) experiment, which is situated on 1500 hectares of boreal forest land, 85 km northwest of Peace River, Alberta (56°44'N, 118°20'W). The main objectives of this large experiment are to provide information useful for maintaining biotic communities, spatial patterns of forest structure, and ecosystem integrity through use of innovative forest harvest and regenerative practices (Chapter 1; Spence *et al.* 1999; Spence and Volney 1999). The EMEND approach seeks to emulate, through variable retention harvest, critical aspects of wildfire and other natural disturbances, and thus maintain structure and function of the pre-harvest forest ecosystem.

The work on parasitoids was conducted in three of four EMEND cover types and employed two of five EMEND harvest treatments as well as unharvested control compartments. We sampled defoliators and their parasitoids from canopy trees in the following cover types: 1) deciduous

dominated (DD) [canopies composed of 70-95% aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.)], 2) conifer dominated (CD) [70-95% white spruce (*Picea glauca* (Moench) Voss)] and 3) deciduous dominated with spruce understory (DU) - as in DD but with understory of white spruce, *Picea glauca*, at least 30% as tall as canopy. Smaller amounts of white birch (*Betula papyrifera* Marsh), black spruce (*Picea mariana* (Mill) BSP), balsam fir (*Abies balsamea* (L.) Mill), and lodgepole pine (*Pinus contorta* Loudon) were also present in the latter two stand types. Defoliators were sampled in 20% residual, 50% residual stands uncut control. There were three replicates of each treatment and control. Harvesting treatments were applied during the winter of 1998-99.

2.3.2 Defoliator and Parasitoid Sampling

We sampled larval populations of lepidopteran defoliators for parasitoids by felling canopy-dominant trees with a chain saw onto a 30 x 50-foot tarpaulin positioned on the ground to catch the crown. Aspen were felled in DD 20%, DD 50%, DD control and DU control compartments. Spruce were felled in CD 20%, CD 50%, and CD control compartments. Additionally, understory spruce were sampled in DU control compartments. Felled trees were of average height and diameter compared to surrounding canopy-dominant trees of the same species, appeared outwardly healthy, had a clear fall path that ensured minimal

disturbance to the canopy, and were at least 50 m from the stand edges and other sample trees.

Sample trees felled in control locations landed on the tarpaulin in natural stand gaps while trees chosen from residual stands were felled from a retention strip onto the tarpaulin in an open machine corridor. During the pre-harvest season (1998), 15 aspen trees were felled June 22-26 and July 23-26; however, most of these were sampled outside of EMEND boundaries and had less than 10 defoliator per tree. All other trees felled in 1998 and 1999 were part of EMEND compartments. Also in 1998, 19 and 18 spruce trees were felled June 8-19 (early) and July 9-17 (late), respectively (Table 2.1). In the post-harvest season (1999) 24 *P. tremuloides* were felled from May 29 to June 10 and 18 *P. glauca* were felled June 20-24 (Table 2.1). Sampling was focused during a short time period for each tree species because defoliator and parasitoid abundance and richness can rapidly change through the season.

Defoliator larvae were collected from felled trees, both by beating randomly selected branches from the crown over a plastic box (approximately 0.75m x 1.5m X 0.3m), and during a timed one person-hour tree and tarpaulin search. Branches were randomly selected from lower, middle and upper crown levels and beaten in the plastic box. Two branches were selected per crown level for aspen and ten 45cm branch tips per level for spruce. The branch beating and timed searches gave an index of overall defoliator abundance. All

defoliators were temporarily held with host foliage in brown paper bags, stored in coolers and transported quickly to the field laboratory for processing.

2.3.3 Defoliator and Parasitoid Rearing

Defoliator larvae and pupae from each sample were sorted to morpho-species (identifications were subsequently confirmed by rearing) and placed in rearing containers. Since most parasitised larvae continue to feed and show no outward appearance of parasitism, all larvae and pupae were reared to determine host-parasitoid relationships and obtain information about parasitoid life history, in addition to confirming host identity. Up to 5 larvae of the same morpho-species or one pupa were reared in separate clear 500 mL plastic cups with fitted, ventilated lids. All larvae were fed fresh foliage from the tree species that they had been collected from; aspen foliage was changed every 3-4 days, and spruce every 5-6 days. Stems of the foliage were wrapped in cotton swabs and fitted snugly into vials of water to maintain foliage turgor and quality. Spruce bud-feeding species were fed a pre-made diet mixture designed for mass rearing spruce budworm (Robertson 1979, Appendix 1). This also worked well for other spruce bud-feeding species. Larvae were checked daily to record development and signs of parasitism.

Parasitoid larvae and pupae were retained in their rearing containers until parasitoids had emerged or pupated and, as they appeared, adult parasitoids with their cocoons were preserved in 75% ethanol for later

identification to species. Host larvae that died without producing parasitoid adults were dissected to ascertain whether parasitoids were present, although such parasitoids could only rarely be identified to species. Defoliators and their parasitoids that did not complete development in one season were held at -3° C in rearing cups placed in black plastic bags from October to January in an attempt to break diapause. Following cold treatment, defoliators and their parasitoids were slowly warmed to 22 °C over 4 days; insect emergence commenced about 2 weeks after warming. Adult lepidopterans were frozen for later pinning and identification and parasitoid adults were preserved in 75% ethanol for later identification. Lepidopteran pupae that did not produce mothes or parasitoids within 3 months after removal from cold treatment were preserved in 75% ethanol and subsequently dissected to determine whether parasitoids were present. Parasitoid pupae from which adults did not emerge were also dissected for evidence of parasitism. Parasitoid presence was established by finding a parasitoid larva or pupa. I identified all reared parasitoids and taxonomists at the Canadian National Collection of Insects, Ottawa, Ontario (Henri Goulet, Gary Gibson, John Huber) and fellow graduate student (Andrew Bennett) verified identification of adult parasitoids. Voucher specimens for both Lepidoptera and Hymenoptera were deposited in the insect collection of the Canadian Forest Service, Northern Forestry Center, Edmonton, Alberta.

All defoliator and parasitoid developmental stages were photographed and these photographs were used to identify live and dead larvae. For abundant defoliator species such as *Operophtera bruceata* (Hulst) and *Choristoneura conflictana* (Wlk.) on aspen, a maximum of 250 larvae were reared per sample tree so as not to exceed our capacity for this labor-intensive work. Percent parasitism for defoliators on each sample tree was calculated using number of parasitised lepidopterans as a proportion of the total number of lepidopterans of that species reared from a particular tree.

2.3.4 Statistical Analyses

Analysis of variance (ANOVA), [General Linear Model (GLM)] was used to analyze the data from the early sample in 1998 for spruce and 1999 for aspen and spruce. Aspen data from 1998 was not analyzed since the trees were not collected on EMEND sites and the target defoliator species were not collected in sufficient numbers to allow analyses. Only trees with greater than 109 defoliator hosts were included for analysis. This model was used to assess the effect of projected harvest treatment, cover type, and sample time for 1998 spruce on parasitoid abundance and richness, host abundance and richness, and lepidopteran host parasitism. Separate ANOVAs were also used to examine harvest treatment effects on parasitoid abundance and richness, host abundance and richness, and lepidopteran host parasitism for both the spruce and aspen data collected in 1999. Finally, ANOVA was used to assess year to

year variation in parasitoid abundance and richness, host abundance and richness, and lepidopteran host parasitism for the spruce data (1998 CD stands were compared with 1999 CD stands).

In addition to analyzing spatial and temporal variation in overall parasitism for all Lepidoptera collected on aspen, *Operophtera bruceata* and *Choristoneura conflictana* were abundant enough on aspen to support separate analyses. Cover type and treatment effects on parasitoid abundance and percent parasitism were analysed for *O. bruceata* and *C. conflictana* with ANOVA. Only variation in overall parasitism rate was analyzed for spruce, as no single defoliator species was sufficiently abundant to be analyzed separately.

Species diversity of host-specific lepidopteran and parasitoid assemblages was measured in several ways to minimize bias due to reliance on single method. Rarefaction estimates were made using internet-based software (Brzuskowski, 1999), and such estimates may be interpreted as a type of diversity measure as they take into account both species richness and abundance. In addition, Simpson's Index, Shannon Index and Hill's reciprocal of Simpson's index were calculated according to Magurran (1988) using Microsoft Excel 2000.

All trees sampled in each compartment were included in calculations of mean parasitoid abundance and richness, total parasitoid richness, and mean host abundance and richness. Trees with greater than 10 defoliators were

included for calculations of parasitoid rarefaction, Shannon Index, Simpson Index, Hill's Index, and lepidopteran host parasitism to provide a better basis for comparison.

All statistics were calculated using SPSS software (SPSS 10.0.5, SPSS Incorporated 1999), except for the 1998 spruce data, which was analyzed using SAS (PROC GLM, SAS Institute 1996). Significance of results was assessed using pair-wise Bonferroni multiple comparison tests for SPSS software, a conservative procedure explicitly designed for dealing with small sample sizes (Zar 1999). For SAS analyses, p- diff tables were used to identify significance of results.

2.4 RESULTS

2.4.1 Parasitoid-host associations and assemblage structure

In all, 5413 lepidopteran larvae and 111 sawfly larvae were reared, representing at least identified species from aspen and 58 species from spruce (Table 2.2). Among these, about 157 morphospecies of Lepidoptera (872 specimens) and 34 morphospecies of sawflies (87 specimens) could not be reliably identified and these are pooled in the "unknown" category for analyses of overall parasitism. Most parasitoid species were uncommon to rare (Table 2.2). Large aspen tortrix, *Choristoneura conflictana* (Wlk.), and Bruce spanworm, *Operophtera bruceata* (Hulst), represented 29.1% and 49.2%, respectively, of reared individual caterpillars collected from aspen. On spruce, a

bud moth, *Zeiraphera unfortunana* Powell, the spruce budworm, *Choristoneura fumiferana* (Clem.), and a needle miner, *Coleotechnites atrupictella* (Dietz), represented, respectively, 46.2%, 10.9% and 10.1% of the overall number of reared hosts.

In total, 470 (c. 8.5%) defoliator larvae were parasitised and adult parasitoids were reared from 251 of these (Table 2.3). The remainder died as larvae and the parasitoids could not be identified. In particular, there was low success in rearing parasitoids from *O. bruceata* as only 7 of 226 parasitised hosts yielded adult parasitoids. Most of the *O. bruceata* parasitoids that developed to emergence were from host pupae. Many *O. bruceata* pupae died during overwintering and any parasitoids present within the puparia also perished. The reared parasitoids included a total of 61 species from defoliators, 57 on Lepidoptera and 4 on sawflies. No parasitoid species was reared from both lepidopterans and sawflies. Of reared parasitoids, 31 species were from hosts on spruce and 31 species from hosts on aspen. The families Braconidae and Ichneumonidae comprised most of my sample and were represented by 25 and 32 species, respectively. The relative diversity of these two families differed only slightly between the two tree species; braconid and Ichneumonid species, respectively, represented 45.2% and 54.8% of parasitoid taxa on aspen and 46.2% and 53.8% of taxa on spruce. Five chalcid species were encountered and these were collected only from hosts on aspen trees.

Affinity to host and tree species varied among parasitoids. Some common parasitoids were polyphagous, usually attacking other hosts on the same tree species (Table 2.3) and these species were mostly braconids. Parasitoids such as *Diadegma* sp. 1, *Glypta* sp. 1, and *Earnius zeirapherae* were collected in relatively high numbers but from only one host and tree species. In contrast, *Apanteles morrisi* and *Campoletis* sp. 1 were collected and reared from several different hosts and both tree species.

One example of multiple parasitism was noted as both *Pteromalis phycidus* Ashmead and one individual of *Sympiesis sericeicornis* (Nees) were reared from an unknown lepidopteran host. Superparasitism was more common and 6 braconid and 6 chalcid parasitoid species were noted to be gregarious. Of these, *Macrocentrus irridescens* French was the most abundant and up to 45 parasitoids were found per host (average was 24.7 ± 2.4). The other gregarious parasitoids were reared in too few numbers to give reliable estimates of number of individuals reared by host. One parasitoid, *Syrphophilus* sp. 1, was reared from an unidentified dipteran host.

2.4.2 Temporal Variation

Seasonal variation in parasitoid assemblages on spruce trees in CD and DU stands could be assessed in 1998 since there were two sample periods, June 8-19 (early) and July 9-17 (late). Mean parasitoid abundance was 25 times higher in the early than in the late samples (Table 2.4A-I; ANOVA:

$F_{1,35}$=76.5, P<0.001), which reflected a similar pattern in host abundance ($F_{1,35}$=69.7, P<0.001). Likewise, mean parasitoid species richness ($F_{1,35}$=17.3, P<0.001) and mean host species richness ($F_{1,35}$=40.8, P<0.001) were also significantly higher earlier in the early season (Table 2.4A-I). The steep slope of rarefaction curves suggest that lepidopterans from both early and late CD and DU stands (Fig. 2.1C) and parasitoids from early CD and DU stands (Fig. 2.1D) were not completely sampled. Fourteen parasitoid species were reared from early samples, in contrast to only two species from late samples. It could not be established whether these two parasitoids from the late sample were also present in the early sample since they were discovered through host dissection and could not be identified to species. It was not possible to compare diversity between early and late sample dates because no trees from the late sample had more than 10 defoliator hosts and therefore failed to give adequate estimates for comparison. Clearly, most of the larvae defoliator activitys in these northern forests occurs before mid-summer.

Parasitoid assemblages from spruce-feeding hosts in CD control stands differed markedly between 1998 (early samples) and 1999 (Table 2.4A-II). Mean parasitoid abundance was significantly higher in 1998 than 1999 ($F_{1,8}$=154.8, P<0.001) as was species richness ($F_{1,8}$=78.9, P<0.001). Similarly, host abundance ($F_{1,8}$=69.7, P<0.001) and species richness ($F_{1,8}$=68.9, P<0.001) was higher in 1998 than 1999 (Table 2.4A-II). This difference mainly reflects the high abundance (localized outbreaks) of *Z. unfortunana* on three CD control

trees in 1998. This species feeds on new buds and shoots of spruce and supports a distinctive parasitoid complex. If the *Z. unfortunana* data are excluded from the analyses year-to-year differences no longer occurs for parasitoid abundance ($F_{1,8}$=0.1, P=0.80), parasitoid species richness ($F_{1,8}$=10.2, P=0.35), host abundance ($F_{1,8}$=0.1, P=0.79), and host species richness ($F_{1,8}$=0.3, P=0.30). Diversity measures indicated that the 1999 parasitoid assemblage was much more diverse than that collected in 1998 when *Z. unfortunana* individuals were included (Table 2.4A-II, Fig. 2.1D). However, when *Z. unfortunana* hosts were removed parasitoid diversity was slightly higher in 1998 than in 1999. Percent parasitism in CD control stands did not differ significantly between years with ($F_{1,8}$=0.0, P=0.89) or without ($F_{1,8}$=1.2, P=0.30) data from *Z. unfortunana* (Table 2.4 A-II).

It was not possible to reliably examine year-to-year variation in aspen. Unfortunately, 1998 was an unusually warm spring and even the earlier, mid-summer sample was phenologically early and yielded few lepidopteran hosts.

2.4.3 Spatial Variation

I) Cover type

There was a significant impact of cover type on pre-treatment parasitoid assemblages in spruce (Table 2.4A-III). Mean parasitoid abundance ($F_{1,35}$=35.9, P<0.001), parasitoid richness ($F_{1,35}$=7.0, P=0.01), and mean host abundance ($F_{1,35}$=35.1, P<0.001) were significantly higher in CD stands than in

DU stands. However, localized outbreaks of *Z. unfortunana* on the three trees in CD stands disproportionately influenced overall patterns; there were no significant differences among cover type for parasitoid abundance ($F_{1,35}$=2.1, P=0.15) and host abundance ($F_{1,35}$=2.9, P=0.10) when these trees were removed from the analysis, although parasitoid richness remained highest in CD stands. CD compartments had higher parasitoid diversity, as measured by the Shannon Index, than DU compartments with or without *Z. unfortunana* individuals included (Table 2.4A-III). In contrast, rarefaction curves suggest that, when adjusted for sample size, diversity was higher in DU than in CD compartments in 1998 although the sampling effort was low (Fig. 2.1B). There was no effect of cover type on parasitism when Z. *unfortunana* data were included (Table 2.4A-III; $F_{1,15}$=0.3, P=0.58).

Cover type comparisons cannot be made for pre-treatment aspen since all trees sampled had too few lepidopteran hosts for analyses. For aspen sampled in 1999, trees from DU compartments supported higher parasitoid abundance ($F_{1,11}$=7.5, P=0.021)), lower host richness ($F_{1,11}$=6.9, P=0.025) than did those from DD compartments (Table 2.4 B-II) *Operophtera bruceata* had higher abundance in DD compared to DU compartments ($F_{1,11}$=23.7, P=0.007) but *C. conflictana* parasitoid abundance was not significantly affected by cover type ($F_{1,11}$=3.1, P=0.11). Parasitism was not affected by cover type for either *O. bruceata* ($F_{1,11}$=1.0, P=0.35) or *C. conflictana* ($F_{1,11}$=1.3, P=0.28). Overall parasitoid diversity was higher in DD than in DU control stands but overall rate

of parasitism was only marginally unaffected by cover type ($F_{1,11}$=4.5, P=0.06) (Table 2.4 B-II).

II) Aspen versus Spruce

In 1999, aspen trees in DD control compartments had higher parasitoid abundance ($F_{1,35}$=35.7, P<0.001), parasitoid richness ($F_{1,35}$=18.8, P<0.001, Fig. 2.3B), host abundance ($F_{1,35}$=209.8, P<0.001) and host richness ($F_{1,35}$=6.7, P=0.015) but lower diversity than spruce in CD control compartments. There was no effect of cover type on percent parasitism ($F_{1,29}$=3.2, P=0.09) (Table 2.4C-I);.

III) Harvesting Treatment

I compared parasitoid assemblages from 1998 among compartments designated for different treatments to assess pre-harvest spatial variation in CD stands (Table 2.4 A-II). Mean parasitoid abundance ($F_{2,35}$=11.0, P<0.001), and host abundance ($F_{2,35}$=17.7, P<0.001) were significantly higher in CD compartments designated as controls (CD-C in Table 2.4 A). Parasitoid diversity was highest in CD 20% residual stands followed by CD control and CD 50% residual compartments (Table 2.4 A-IV, Fig. 2.2 B). Diversity estimates were not calculated for most DU stands.

When *Z. unfortunana* data are excluded from the analysis, host abundance ($F_{2,35}$=0.03, P=0.96), parasitoid abundance ($F_{2,35}$=1.9, P=0.17), host

richness ($F_{2,35}$=1.1, P=0.36) and parasitoid richness ($F_{2,35}$=1.4, P=0.28) did not differ significantly among CD control, CD 20% and CD 50% residual compartments. These parasitoid richness measures were calculated from minimal data and thus the above test was not robust. Diversity indices could not be calculated for CD control compartments after removing *Z. unfortunana* individuals since there was only one parasitoid reared from another defoliator species.

For spruce understory trees in DU stands, there was marginally significant spatial variation for pre-treatment percent parasitism with *Z. unfortunana* individuals included (Table 2.4 A-IV, $F_{2,15}$=3.7, P=0.048). After *Z. unfortunana* individuals were removed from control sites, host parasitism differed significantly between compartments but there was no apparent trend reflecting intensity of harvesting treatments ($F_{2,15}$=5.6, P=0.023).

There was an insignificant effect of treatment on host richness ($F_{2,17}$=2.6, P=0.11) and parasitoid abundance ($F_{2,17}$=4.8, P=0.024) for spruce CD stands in 1999; however, parasitoid richness ($F_{2,17}$=0.4, P=0.70), defoliator abundance ($F_{2,17}$=2.0, P=0.18) or percent parasitism ($F_{2,17}$=0.8, P=0.46) were significantly affected (Table 2.4A-V). Unharvested CD control compartments had higher parasitoid diversity than CD 50% residual stands; however diversity indices could not be calculated for CD 20% residual stands because there were too few parasitoids (Table 2.4B-V, Fig. 2.2D).

Rarefaction estimates for spatial variation provide a revealing view of the quantity of data collected. The curve for 1998 CD compartments was similar to 1999 CD compartments but spruce trees from DU compartments were not sampled well enough to fully capture the greater lepidopteran diversity (Fig. 2.1A). Similarly, 1998 CD and DU and 1999 CD compartments suggest that parasitoid diversity was not fully captured (Fig. 2.1B). Post-treatment lepidopteran and parasitoid diversity were also measured and the rarefaction curves indicate that both CD control communities were moderately well sampled in 1998 (Fig. 2.2A,B) and 1999 (Fig 2.2C,D) but 20% and 50% residual and DU compartments needed additional sampling to estimate diversity reliably in 1998 (Fig. 2.2A,B) and 1999 (Fig. 2.2C,D).

In post-treatment aspen (DD) compartments there was significantly higher host richness in controls compared to 50% residual compartments ($F_{3,23}$=4.1, P=0.021) (Table 2.4B-III). Abundance of parasitoids in *O. bruceata* and *C. conflictana* was not affected by treatment ($F_{1,17}$=3.6, P=0.77 and $F_{1,17}$=0.6, P=0.55, respectively). The highest parasitoid diversity occurred in DD 50% residual compartments and, interestingly, DD control compartments had the lowest diversity (Table 2.4B-III, Fig. 2.3D). Parasitism was not affected by treatment for either *O. bruceata* ($F_{1,17}$=0.8, P=0.49) or *C. conflictana* ($F_{1,17}$=1.9, P=0.18).

Rarefaction curves demonstrate that aspen from both DD and aspen collected from DU stands were reasonably sampled for lepidopterans (Fig.

2.3A) but not their parasitoids (Fig. 2.3B). Similarly, Lepidoptera collected from all aspen treatments in 1999 were well sampled (Fig. 2.3C) but additional sampling was needed to get an accurate picture of their parasitoid assemblages (Fig. 2.3D).

2.5 DISCUSSION

Although parasitic Hymenoptera are held to be highly sensitive to disturbance, few studies have used this taxon to assess the impact of environmental changes associated with silviculture (Lewis and Whitfield 1999), possibly because of a huge taxonomic impediment. Nonetheless, these organisms can provide valuable insight about forest ecosystems, particularly on a fine scale (LaSalle 1993) and from a functional perspective; parasitoids are central to the environmental resistance that controls potentially serious forest pests.

In this study, I have identified some of the parasitoid–host relationships potentially key to boreal forest ecosystem dynamics. However, the steep slopes of rarefaction curves suggest that even an uncommonly strenuous effort was insufficient to sample larval defoliator species diversity thoroughly enough to support solid conclusions about the composition of the parasitoid communities. This work does concur, however, with Le Corff *et al.* (2000) in showing that the spring/early summer defoliator fauna is most abundant and has the most plentiful and diverse parasitoid community.

There are few studies on parasitoid communities (Le Corff *et al.* 2000) or food webs (Memmott and Godfray 1993) that include parasitoids so as to allow comparison to my study. For example: larval parasitism by all parasitoids in the guild *for Zeiraphera canadensis* (Lepidoptera: Tortricidae) had been recorded in Eastern Canada ranging between 2% and 12.4% (Turgeon 1992), in Delaware *Diacrisia virginica* (Lepidoptera: Arctiidae) were collected and reared to reveal larval parasitism rates between 0 and 33% (Raffa 1977) and parasitism in endemic *Malacosoma disstria* (Lepidoptera: Lasiocampidae) population in Alberta ranged between 8% and 17% for all parasitoid species combined (Parry 1995). Thus, 8% parasitism for aspen and spruce defoliating lepidopterans was similar to studies across North America. Previous studies that examined the parasitoid complexes for *C. conflictana* (Anonomous 1974, Prentice 1955), *O. bruceata* (Brown 1962) and *C. fumiferana* (Williams 1994) indicate that parasitoid species collected during the tree sampling was not a full estimate of the known parasitoids.

This study also has demonstrated that parasitoid assemblages differ between tree species and that they can show variation between cover types. Parasitoid communities differed conspicuously between *P. tremuloides and P. glauca* (Table 2.2, 2.3C). This result was expected as host defoliator species feed on a narrow range of host plant(s) (Ives and Wong 1988, Pedigo 1989) and many parasitoid species specialize in one or more closely related insect host species and feeding niche (Hawkins 1993, 1994, Hawkins and Lawton

1987, Hochberg and Hawkins 1992). Thus, defoliator populations are generally restricted to host tree species and parasitoid distributions are generally restricted to their insect host locations. Interestingly, the *P. glauca* parasitoid community was more diverse than that from *P. tremuloides*. Hawkins and Lawton (1987) and Gross (1993) have demonstrated that concealed hosts were less vulnerable to parasitoids. Perhaps *P. tremuloides*, which has a large fauna of leaf rollers and leaf-tiers, supports more concealed feeding lepidopterans compared to *P. glauca* communities and, therefore, supported a lower parasitoid diversity.

Parasitoid assemblages, parasitoid abundance and species richness also differed noticeably for the same tree species and defoliator species between different cover types. Most of the parasitoid species reared from my study were singletons and revealed that sampling effort could be improved, however parasitism did not differ significantly so it was difficult to generalize about parasitoid community structure and the effect on parasitism. For spruce trees, parasitoid abundance and richness was higher in CD stands than in DU stands and this likely reflected significantly higher defoliator abundance on spruce in CD compartments compared to DU compartments. Interestingly, parasitoid diversity was somewhat higher on spruce sampled from DU locations although percent parasitism did not differ significantly between sites. On aspen trees, parasitoid abundance was significantly higher in DU stands compared to DD stands but richness and percent parasitism did not differ.

Le Corff *et al.* (2000) also noted differences in parasitoid communities between sites but there is some literature to suggest factors that account for this sort of spatial variation in forest settings. Differences among parasitoid species in fecundity, host-finding technique, and reproductive strategy could account for differences in parasitism across cover types (Askew 1971). Such information could be usefully built into management to maximize impacts of natural enemies in pest population regulation. For example, *P. glauca* defoliators tended to be less abundant on spruce trees remaining after overstory aspen harvest and this may have promoted higher levels of parasitism (Heads and Lawton 1982; Morrison *et al.* 1980; Morrison and Strong 1981).

There were few impacts of harvesting treatment on parasitoids. Overall parasitism did not differ among trees in compartments allocated to different treatments pre- or post- harvest either for *P. glauca* or *P. tremuloides*. Furthermore, data about parasitism of *O. bruceata* and *C. conflictana* also indicated no response to treatment. This result was likely due to minimal impact on relative magnitudes of host and parasitoid populations during harvesting. As individuals of both taxa overwinter either in duff near the tree base or in host tree foliage (Ives and Wong 1988; Peterson and Peterson 1992), low impact winter harvest with compaction and vehicular traffic confined to machine corridors (Sidders and Spence 1999) should have minimized effect

on these insect populations. Thus, individuals from the previous year's populations were not greatly affected by treatment levels.

Factors such as increased solar radiation (Paquin and Coderre 1997) over time may alter host-parasitoid relationships (e.g., Roland and Taylor 1997, Shapiro and Pickering 2000). Other studies such as that of Paquin and Coderre (1997) found that some groups of macroarthropods (such as Diplopoda and Pseudoscorpionida) were affected one year post clear-cut while other groups were seemingly unaffected. Some insect populations need an adjustment period before populations differ in abundance and composition after disturbance. Thus differences may become apparent in subsequent years following harvest which requires additional study. My work provides a strong baseline from which such studies may be launched.

2.6 REFERENCES

Anonomous. 1974. Parasitoids associated with the large aspen tortrix in Alaska. *Can. Ent.* **106**:1248-1250.

Askew, R. R. 1971. Parasitic insects. Heinemann Educational Books, London.

Brown, C.E. 1962. The life history and dispersal of the Bruce Spanworm, *Operophtera bruceata* (Hulst), (Lepidoptera: Geometridae). *Can Ent.* **94**: 1103-1107.

Brzuskowski, J. 1999. Rarefaction calculator.

http://www.biology.ualberta.ca/jbrzusto/rarefact.php

Buddle, C.M., J.R. Spence and D.W. Langor. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. *Ecography.* **23**: 424- 436.

Gross, P. 1993. Insect behavioral and morphological defenses against parasitoids. *Ann. Rev. Entomol.* **38**: 251-273.

Hawkins, B.A. 1993. Parasitoid species richness, host mortality and biological control. *Am. Nat.* **141:** 634.641.

Hawkins, B.A. 1994. Pattern and process in host-parasitoid interactions. Cambridge University Press, Cambridge.

Hawkins, B.A. and J.H. Lawton. 1987. Species richness for parasitoids of British phytophagous insects. *Nature*: **326**:788-790

Heads, P.A. and J.H. Lawton. 1982. Studies on the natural enemy complex of the holly leaf –miner: the effects of scale on the detection of aggressive responses and the implication for biological control. *Oikos* **40**: 267- 276.

Hochberg, M.E. and B.A. Hawkins. 1992. Refuges as a predictor of parasitoid diversity. *Science*. **255**: 973-976.

Huhta, V. 1971. Succession in the spider communities if the forest floor after clear-cutting and prescribed burning. *Ann. Zool. Fenn.* **8:** 483-542.

Ives, W.G.H. and H.R. Wong. 1988. Tree and shrub insects of the Prairie Provinces. Can. For. Serv., North. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-292.

Janzen, D.H. 1981. The peak in North American Ichneumonid species riches lies between 38° and 42°N. *Ecology*. **62**: 532 – 537.

Janzen, D.H. and C. Pond. 1975. A comparison, by sweeping, of the arthropod fauna of secondary vegetation in Michigan, England, and Costa Rica. *Trans. Royal Entomol. Soc. London*. **127**: 33 – 50.

Kruess, A. and T. Tscharntke. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicea sepium*. *Oecologia*. **122**: 129- 137.

LaSalle, J. 1993. Parasitic Hymenoptera, Biological Control and Biodiversity. *In*: Hymenoptera and Biodiversity (LaSalle, J. and I.D. Gauld, eds.), CAB International, Wallingford, pp. 197-215.

LaSalle, J., I.D. Gauld. 1992. Hymenoptera: Their diversity, and their impact on the diversity of other organisms. *In*: Hymenoptera and Biodiversity (LaSalle, J. and I.D. Gauld, eds.), CAB International, Wallingford, pp. 1-26.

LaSalle, J. and I.D. Gauld. 1993. Parasitic Hymenoptera and the biodiversity crisis. *Redia*. **74**: 315- 334.

Lewis, C.N. and J.B. Whitfield. 1999. Braconid wasp (Hymenoptera: Braconidae) diversity in forest plots under different silvicultural methods. *Community and Ecosystem Ecol.* **28** (6): 986- 993.

Le Corff, J., R.J. Marquis, J.B. Whitfield. 2000. Temporal and spatial variation in a parasitoid community associated with the herbivores that feed on Missouri *Quercus*. *Env. Entomol.* **29(2)**: 181-194.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton.

Memmott, J. and H.C.G. Godfray. 1993. Parasitoid webs. *In*: Hymenoptera and Biodiversity (LaSalle, J. and I.D. Gauld, eds.), CAB International, Wallingford, pp. 217- 234.

Morrison, G., W.J. Lewis and D.A. Nordlund. 1980. Spatial differences in *Heliothis zea* egg density and the intensity of parasitism by *Trichogramma* spp.: an experimental analysis. *Environ. Ent.* **9:** 79- 85.

Morrison, G. and D. Strong. 1981. Spatial variation in egg density and the intensity of parasitism in a neotropical chrysomelid (Cephaloleia *consanguinea*). *Ecol. Ent.* **6:** 55- 61.

Niemela, J. D.W. Langor and J.R. Spence. 1993. Effects of clear-cut harvesting on boreal ground beetle assemblages (Coleoptera: Carabidae) in Western Canada. *Conserv. Biol.* **7**(3): 551-561.

Owen, D.F. and J. Owen. 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature.* **249**: 583- 584.

Paquin, P. and D. Coderre. 1997. Deforestation and fire impact on edaphic insect larvae and other macroarthropods. *Env. Entomol.* **26(1):** 21-30.

Parry, D. 1995. Larval and pupal parasitism of the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), in Alberta, Canada. *Can. Ent.* **127**: 877-893.

Pedigo, L.P. 1989. Entomology and pest management. Macmillan Publishing Company, New York, New York.

Peterson E.B. and N.M Peterson. 1992. Ecology, management, and the use of aspen and balsam poplar in the prairie provinces, Canada. For. Can., Northwest Reg., North. For. Cent., Edmonton, Alberta. Spec. Rep. 1.

Powell, A.H. and G.V.N. Powell. 1987. Population dynamics of male euglossine bees in Amazonian forest fragments. *Biotropica.* **19**: 176-179.

Prentice, R.M. 1955. The life history and some aspects of the ecology of the large aspen tortrix, *Choristoneura conflictana* (Wlkr.) (N. Comb.) (Lepidoptera: Tortricidae). *Can Ent.* **87**: 461-473.

Raffa, K.F. 1977. Potential alternate hosts of the Gypsy moth parasite *Apanteles porthetriae. Env. Ent.* Feb: 57-59.

Robertson, J.L. 1979. Rearing the western spruce budworm. USDA. Washington, DC.

Roland, J. and P.D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature.* **386**: 710 – 713.

SAS Institute. 1996. SAS for UNIX, version 6.2. SAS Institute, Cary, NC.

Shapiro, B.A. and J. Pickering. 2000. Rainfall and parasitic wasp (Hymenoptera: Ichneumonidae) activity in successional forest stages at Barro Colorado Nature Monument, Panama and La Selva Biological Station, Costa Rica. *Agric. For. Entomol.* **2:** 39-47.

Sidders, D and J.R. Spence. 1999. Ecosystem management emulating natural disturbance: research study and field guide. Can. For. Serv. Unpubl. Rep.

Spence, J.R. and W.J. Volney. 1999. EMEND- Ecosystem management emulating natural disturbance. Sustainable For. Manag. Network Proj. Rept. 1999-14.

Spence, J.R., W.J.A. Volney, V.J. Leiffers, M.G. Weber, S.A. Luchkow, and T.W. Vinge. 1999. The Alberta EMEND project: Recipe and cook's argument. *In:* Science and practice: sustaining the boreal forest (T.S. Veeman et al, eds.), SFM Network, 14-17 Feb. 1999, Edmonton, pp. 583- 590.

S.P.S.S. version 10.0.5. 1999. S.P.S.S. Incorporated.

Szujecki, A. 1972. Impact of clearcutting on the soil entomofauna, pp. 4305-4309. *In:* Contribution in the seventh world forestry congress, No. 3. Buenos Aries, Argentina.

Turgeon, J.L. 1992. Status of research on the development of management tactics and strategies for the spruce bud moth in white spruce plantations. *For. Chron.* **68(5)**: 614-622.

Williams. D.J.M. 1994. Rearing parasitoids of the spruce budworm from Northern Alberta. Nat. Res. Can., For. Manage. Note 61. 4pp.

Zar, J.H. 1999. Biostatistical analysis. Prentice Hall, Engelwood Cliffs, New Jersey.

Zuidema, P.A., J.A. Sayer and W. Dijkman. 1996. Forest fragmentation and biodiversity: the case for intermediate- sized conservation areas. *Env. Conserv.* **23**(4): 290 -297.

Table 2.1. Number of aspen and spruce trees sampled in each treatment pre - (1998) and post - (1999) harvest and stand type used in analysis.

Treatment		DD	DU	CD
20% Residual	Pre		Early Spruce - 3 *Late Spruce - 3	Early - 4 *Late - 3
	Post	Aspen - 6		Spruce - 6
50% Residual	Pre		Early Spruce - 3 *Late Spruce - 3	Early – 3 *Late – 3
	Post	Aspen - 6		Spruce - 6
Control	Pre		Early Spruce - 3 *Late Spruce - 3	Early – 3 *Late – 3
	Post	Aspen - 6	Aspen - 6	Spruce - 6

* = No trees sampled had >10 Lepidoptera larvae hosts and these trees could not be included in statistical analysis.

Table 2.2. Lepidoptera and sawfly hosts reared from aspen and spruce in 1998 and 1999. Stand abbreviations are: DD- deciduous dominated; CD- conifer dominated; and DU-A and DU-S are aspen and spruce respectively sampled from deciduous dominated with spruce understory.

Taxon	Abbreviation	Host	No. Reared	No. Parasitized	Stand Type
Lepidoptera					
Gelechidae					
Coleotechnites atrupictella (Dietz)	Coat	spruce	139	4	CD
Geometridae					
Itame sp.	Itsp	aspen	7	2	DD
Metanema inatomaria Guenee	Mein	aspen	1	1	DD
Operophtera bruceata (Hulst)	Opbr	aspen	1970	226	DD,DU-A
Noctuidae					
Egira delosa (Grote)	Egde	aspen	9	1	DU-A
Enargia infumata (Grt.)	Enim	aspen	46	7	DD
Feralia jacosa (Guenee)	Feja	spruce	6	1	CD
Notodontidae					
Clostera brucei Edwards	Clbr	aspen	2	1	DD
Papilioidae					
Papilio canadensis R & J	Paca	aspen	5	1	DD
Tortricidae					
Acleris variana (Fern.)	Acva	spruce	81	4	CD-DU-S
Choristoneura conflictana (Wlk.)	Chco	aspen	1187	148	DD, DU-A
Choristoneura fumiferana (Clemens)	Chfu	spruce	149	8	CD
Zeiraphera fortunana (Kft.)	Zefo	spruce	8	2	CD
Zeiraphera unfortunana Powell	Zeun	spruce	630	37	CD, DU-S
Unknown Lepidoptera	Lepid	Spruce. aspen	872	23	DD, CD, DU-A. DU-S
Symphyta	Symp	Spruce. aspen	87	4	DD, CD, DU-S
Hymenoptera Reared	Unkn	spruce. aspen		42	DD, CD, DU-A. DU-S

Table 2.3. Parasitoids reared from Lepidoptera and Symphyta defoliators of spruce and aspen in 1998 and 1999.

Parasitoid[1]	No. Specimens[2]	Host[3,4]	Tree	Stand Type[5]
Braconidae				
Aleoides nr. *autograohae* (Viereck)	1	Lepid(1)	spruce	DU-S
Aleoides palmatus (Walley)	14	Chco(1), Clbr(1), Enim(7), Itsp(2), Mein(1), Unkn(2)	aspen	DD
Aleoides scrutator (Say)	1	Opbr(1)	aspen	DD
Apanteles aristoteliae Viereck	1	Lepid(1)	spruce	CD
Apanteles morrisi Mason	3	Unkn(2), Acva(1)	aspen, spruce	DD, Du-S
Apanteles sp. 1	3	Unkn(2), Chco(1)	aspen	DD
Apanteles sp. 2	4	Opbr(1), Chco(2), Unkn(1)	aspen	DD, DU-A
Apanteles sp. 3	4	Unkn(4)	aspen	DD, DU-A
Apanteles starki Mason	1	Acva(1)	spruce	CD
Ascogaster provancheri Dalla Torre	1	Lepid(1)	spruce	CD
Bassus annulipes (Cresson)	48	Chco(43), Lepid(3), Unkn(1), Opbr(1)	aspen	DD, DU-A
Clinocentrus sp. 1	2	Acva(1), Zefu(1)	spruce	CD, DU-S
Clinocentrus sp. 2 nr. *mellipes* (Ash.)	12	Zeun(12)	spruce	CD, DU-S
Cotesia acauda (Provancher)	1	Lepid(1)	spruce	DU-S
Cotesia hemileucae Riley	1	Lepid(1)	aspen	DD
Dolicogenidea absona (Muesebeck)	4	Chfu(3), Zeun(1)	spruce	CD
Earnius zeirapheriae Walley	11	Zeun(11)	spruce	CD, DU-S
Glyptapanteles flavovariatus (Mues.)	1	Symp(1)	spruce	CD
Homolobus flagitator (Curtis)	1	Symp(1)	spruce	CD
Macrocentrus iridescens French	48*	Chco(42), Unkn(5), Lepid(1)	aspen, spruce	DD, DU-S, DU-A
Macrocentrus nr. *iridescens* Trench	1*	Opbr(1)	aspen	DD
Macrocentus nigridorsis Viereck	2*	Lepid(2)	aspen, spruce	DD,CD
Meteorus nr. *bakeri* Cook and Davis	1	Chco(1)	aspen	DD
Meteorus hicoriae Muesebeck	4	Coat(4)	spruce	CD
Meteorus trachynotus Viereck	1	Chco(1)	aspen	DD

Parasitoid[1]	No. Specimens[2]	Host[3,4]	Tree	Stand Type[5]
Ichneumonidae				
Agrypon flaveolatum (Gravenhorst)	3	Opbr(1), Lepid(2)	aspen, spruce	DD,CD
Apechthis picticornis (Cresson)	2	Chco(2)	aspen	DD
Banchinae	1	Zeun(1)	spruce	CD
Campoletis sp. 1	3	Zeun(2), Opbr(1)	aspen, spruce	DD,CD
Campopleginae	2	Lepid(1), Egde(1)	aspen, spruce	CD, DU-A
Campoplex sp. 1	1	Unkn(1)	aspen	DU-A
Campoplex sp. 2	2	Zeun(1), Zefo(1)	spruce	CD
Campoplex or *Venturia*	1	Zeun(1)	spruce	CD
Ctenopelmatinae or Orthocentrinae	1	Lepid(1)	spruce	CD
Diadegma sp. 1	11	Chco(11)	aspen	DD, DU-A
Diadegma sp. 2	1	Unkn(1)	spruce	DU-S
Diadegma sp. 3	1	Acva(1)	spruce	CD
Diadegma sp. 4	5	Zeun(5)	spruce	CD
Diadegma sp. 5	1	Unkn(1)	aspen	DD
nr. *Diadegma*	1	Opbr(1)	aspen	DU-A
Exochus sp. 1	1	Symp(1)	aspen	DD
Glypta sp. 1	14	Chco(14)	aspen	DD,DU-A
Glypta sp. 2	1	Unkn(1)	aspen	DD
Ichneumoninae	5	Lepid(5)	spruce	CD
Mesochorus sp. 1	4	Zeun(4)	spruce	CD
Mesochorus sp. 2	1	Feja(1)	spruce	CD
Mesochorus sp. 3	1	Chfu(1)	spruce	CD
Mesochorus sp. 4	1	Opbr(1)	aspen	DU-A
Phydietus sp. 1	1	Acva(1)	spruce	DU-S
Triclistus podagricus (Gravenhorst)	2	Lepid(2)	aspen	DD,DU-A
Tromatobia ovivora (Boheman)	6	Unkn(6)	aspen, spruce	DD,CD,DU-S
Tryphonae or Ctenopelmatinae	1	Symp(1)	spruce	DU-S

Parasitoid[1]	No. Specimens[2]	Host[3,4]	Tree	Stand Type[5]
Eulophidae				
Eulophus sp. 1	1*	Paca(1)	aspen	DD
**Sympiesis sericeicornis*(Nees)	2*	Unkn(1)	aspen	DD
Pteromalidae				
Mesopolobus tortricis (Brues)	1*	Chco(1)	aspen	DD
Mesopolobus verditer (Norton)	1*	Lepid(1)	aspen	DD
Pteromalis phycidis Ashmead	1*	Unkn(1)	aspen	DD

1. * = superparasitoid
2. * = gregarious
3. refers to Table 2.2 for taxon abbreviations
4. Numbers in parentheses refer to number of specimens
5. DD = deciduous dominated, CD = conifer dominated, DU-A = aspen from overstory, DU-S = spruce from understory

Table 2.4. Summary of lepidopteran hosts and parasitoid abundance, species richness and species diversity from samples collected in DD, CD, and DU cover types from a) spruce, b) aspen and c) post-treatment aspen and spruce. Comparisons with the different letters denote statistical significance.

A. Spruce			Parasitoids							Lepidoptera Hosts			
Scale	Sample	No. trees sampled	Mean Abundance per Tree	Total Species Richness	Mean Richness per tree	Parasitoid Rarefaction	Shannon Index (H)	Simpson Index (1-C)	Hill's Index (N2)	Mean Abundance	Total Richness	Mean Richness	Proportion Parasitized
I- 1998	Early	19 (16)	10.0±0.75[b]	14	1.8±0.25[b]	15.1±0.82 (40)	2.35	0.88	7.37	43.7±3.33[b]	65	9.1±0.64[b]	0.30.05
Temporal	Late	17 (0)	0.4±0.79[a]	2	0.3±0.27[a]	NE	NE	NE	NE	3.1±3.54[a]	40	3.1±0.66[a]	NE
II- Year	1998 Early	3 (3)	31.7±0.38[b]	10	4.7±0.33[b]	5.0± 0.90(10)	1.66	0.81	5.25	152.0±20.96[b]	59	9.6±2.33[b]	0.2±0.05[a]
Temporal	1998 Early(-Z)	3(3)	2.7±1.04	10	2.7±0.67	7.7±1.03 (10)	2.48	0.94	16.67	24.7±5.30		8.3±1.45	0.1±0.06
	1999	6 (6)	3.0±0.74[a]	12	1.8±0.48[a]	7.9±0.87 (10)	2.28	0.92	12.36	22.5±4.46[a]	22	6.3±1.02[a]	0.2±0.04[a]
III- =1998	CD	19 (9)	8.5±0.75[b]	12	1.5±0.25[b]	3.9±0.61 (5)	2.12	0.83	7.40	37.8±3.33[b]	33	6.0±0.64[a]	0.3±0.03[a]
Spatial	CD (-Z)	19 (9)	3.9±1.10	10	1.2±0.40	4.3±0.66(5)	2.19	0.93	13.91	17.4±4.11	33	5.9±0.88	0.2±0.04
	DU	17 6)	1.9±0.79[a]	10	0.5±0.27[a]	5.0±0.00 (5)	1.95	NE	NE	9.0±3.54[a]	51	6.1±0.68[a]	0.3±0.03[a]
IV- 1998	Overall												
Spatial	CD-C	6 (3)	16.3±1.32[c]	7	2.3±0.44[a]	1.8±0.39 (2)	1.66	0.81	5.25	78.0±35.00[b]	24	6.7±1.14[a]	0.2±0.00[a]
	CD-C (-Z)*	6 (3)	1.8±1.07	1	1.3±0.46	NE	NE	NE	NE	14.3±4.19	24	5.8±1.14	0.1±0.05
	CD-20	7 (3)	4.5±1.24[b]	11	1.7±0.42[a]	1.9±0.22 (2)	2.21	0.85	19.50	17.3±5.52[a]	27	5.9±1.07[a]	0.3±0.06[a]
	CD-50	6 (3)	4.5±11.32[ab]	3	0.5±0.44[a]	1.8±0.37(2)	1.04	0.83	6.00	18.2±5.90[a]	30	5.5±1.14[a]	0.3±0.06[a]
	DU-C	5 (3)	2.4±1.48[ab]	4	1.1±0.50[a]	2.0±0.00 (2)	1.39	NE	NE	7.3±6.59[a]	12	4.7±1.27[a]	0.4±0.06[a]
	DU-20	6 (1)	0.8±1.32[a]	1	0.2±0.44[a]	NE	NE	NE	NE	8.3±5.90[a]	16	5.3±1.14[a]	NE
	DU-50	6 (3)	2.5±1.32[ab]	2	0.3±0.44[a]	2.0±0.00 (2)	0.69	NE	NE	11.3±5.90[a]	30	8.3±1.14[a]	0.2±0.06[a]
V- 1999	All hosts												
Spatial	CD-C	6 (6)	3.0±1.05[a]	9	1.8±0.35[b]	1.9±0.24 (2)	2.09	0.84	16.50	22.5±5.03[a]	19	6.3±0.96[a]	0.2±0.04[a]
	CD-20	6 (3)	2.3±1.05[a]	1	0.2±0.35[a]	NE	NE	NE	NE	14.7±5.03[a]	11	4.5±0.96[a]	0.1±.06[a]
	CD-50	6 (3)	1.3±1.05[a]	3	0.7±0.35[ab]	2.0±2.00 (2)	1.04	0.83	6.00	9.8±5.03[a]	8	3.5±0.96[a]	0.3±0.06[a]

* CD-C stand without *Zeiraphera unfortunana* larvae

B. Aspen		Parasitoids								Lepidoptera Hosts			
Scale	Sample	No. trees sampled	Mean Abundance per Tree	Total Species Richnes	Mean Richnes s per	Parasitoid Rarefaction	Shanno n Index (H)	Simpson Index (1-C)	Hill's Index (N2)	Mean Abundance	Total Richness	Mean Richness	Proportion Parasitized
I- Year	1999	24	15.8±1.58	18	2.8±0.52	5.0±1.10 (10)	1.91	0.79	4.82	117.1±7.35	29	6.08	0.1±0.02
II- 1999	DD	6 (6)	14.5±2.07[a]	15	2.8±0.27[a]	3.39±0.83 (5)	1.67	0.79	4.79	124.8±17.95[a]	27	8.2±0.99[b]	0.1±0.02[a]
Spatial	DU	6 (6)	22.5±2.07[b]	8	3.5±0.27[a]	3.2±0.76 (5)	1.60	0.77	4.42	109.8±17.95[a]	10	4.5±1.99[a]	0.2±0.02[b]
III- 1999	Overall												
Spatial	DD-C	6 (6)	14.5±2.31[b]	7	2.8±0.52[a]	1.74±0.44 (2)	1.53	0.74	3.91	124.8±14.83[a]	17	8.2±0.86[b]	0.1±0.02[a]
	DD-20	6 (6)	7.0±2.31[a]	7	2.2±0. 52[a]	1.8±0.74 (2)	1.54	0.76	4.20	132.2±14.83[a]	13	6.8±0.86[ab]	0.1±0. 02[a]
	DD-50	6 (6)	12.2±2.31[b]	10	2.7±0. 52[a]	1.8±0.40 (2)	1.79	0.80	4.93	101.7±14.83[a]	18	4.8±0.86[a]	0.1±0. 02[a]
	DU-C	6 (6)	22.5±2.31	8	3.5±0. 52	1.8±0.42 (2)	1.60	0.77	4.42	109.8±14.83	10	4.5±0.86	0.2±0.02
IV-1999	*O. bruceata*	24	9.01.34	9	3.3±0.54	NE	NE	NE	NE	63.7±4.82	-	-	0.1±0.02
	C. conflictana	24	6.2±0.89	8	9.9±1.35	1.7±0.45(2)	1.43	0.71	3.50	42.5±4.91	-	-	0.1±0.02

C. Aspen and Spruce		Parasitoids								Lepidoptera Hosts			
Scale	Sample	No. trees sampled	Mean Abundance per Tree	Total Species Richnes	Mean Richnes s per	Parasitoid Rarefaction	Shanno n Index (H)	Simpson Index (1-C)	Hill's Index (N2)	Mean Abundance	Total Richness	Mean Richness	Proportion Parasitized
I- Control	Aspen	18 (18)	11.2±1.07[b]	18	2.6±0.27[b]	4.96±1.10 (10)	1.91	0.79	4.79	119.6±5.07[b]	29	6.6±0.50[b]	0.1±0.03[a]
Spatial	Spruce	18 (12)	2.2±1.07[a]	12	0.9±0. 27[a]	7.90±0.87 (10)	2.27	0.92	12.36	15.7±5.07[a]	22	4.8±0.50[a]	0.2±0.04[a]

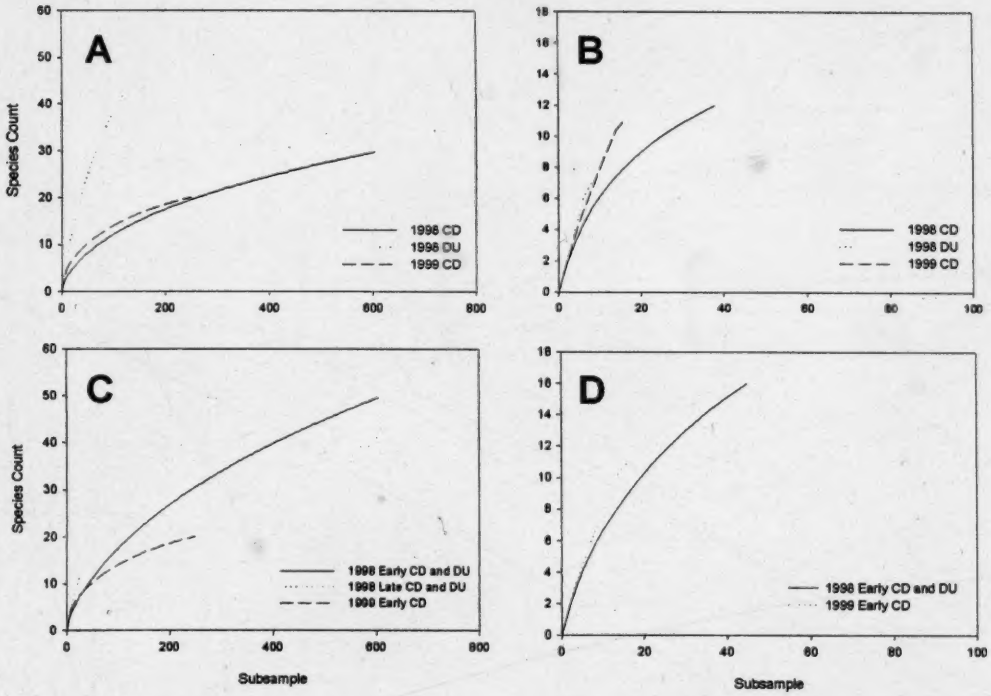

Figure 2.1. Rarefaction curves for Lepidoptera and parasitic Hymenoptera species collected from *P. glauca* trees felled in CD and DU stands. Comparisons were made between A) 1998 and 1999 CD and DU Lepidoptera and B) parasitoids reared; C) combined early and late 1998 and 1999 Lepidoptera and D) parasitoids reared CD and DU control locations.

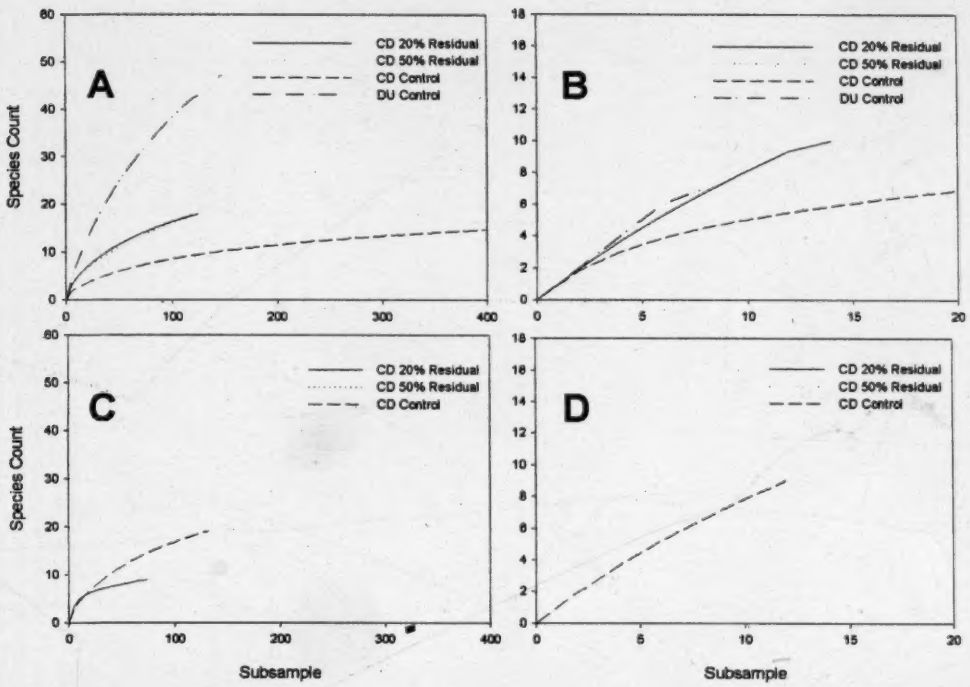

Figure 2.2. Rarefaction curves for Lepidoptera and parasitic Hymenoptera species collected from *P. glauca* trees felled in CD and DU stands. Comparisons were made between A) early 1998 Lepidoptera and B) parasitoids reared from CD and DU stands; C) 1999 Lepidoptera and D) parasitoids reared CD stands.

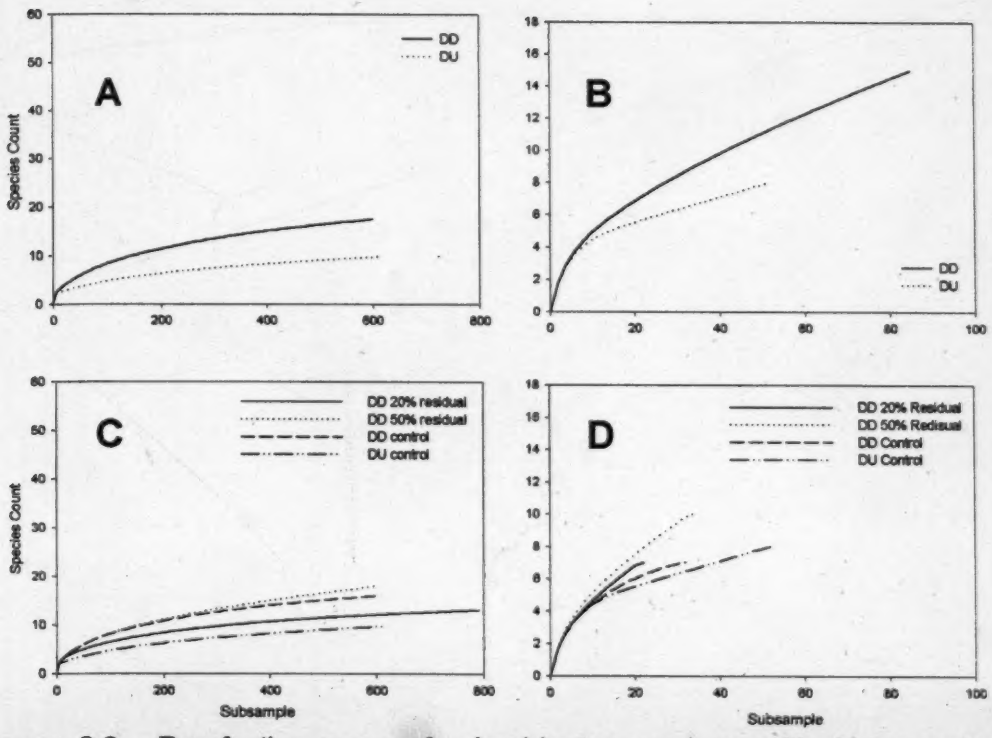

Figure 2.3. Rarefaction curves for Lepidoptera and parasitic Hymenoptera species collected from post- treatment *P. tremuloides* trees felled in DD and DU stands. Comparisons were made between A) Lepidoptera and B) parasitoids reared from DD and DU stands; C) Lepidoptera and D) parasitoids reared from DD 20% and 50% residual treatments and DU control locations.

Chapter 3

THE IMPACTS OF VARIABLE RETENTION HARVESTING ON SPRUCE BEETLE (*DENDROCTONUS RUFIPENNIS*) PARASITOIDS

3.1 SYNOPSIS

The community of parasitoids that use *Dendroctonus rufipennis* (Kirby) in northwestern Alberta was assessed by sampling beetle-infested *P. glauca* (Moench) Voss bolts that were translocated into control and harvested stands immediately after variable retention logging (1999 – 2000). Four parasitoid species were reared from *D. rufipennis* larvae using a novel agar based media. *Coeloides rufovariegatus* (Provancher) (Ichneumonoidea: Braconidae) was the most common parasitoid, *Bracon tenuis* Muesebeck & Walley (Ichneumonoidea: Braconidae) was the second most abundant parasitoid and was reared more successfully than *C. rufovariegatus*. Smaller proportions of beetles were parasitised by *Roptrocerus xylophagorum* (Ratzeburg) (Chalcidoidea: Pteromalidae) and *Dinotiscus dendroctoni* (Ashmead) (Chalcidoidea: Pteromalidae). Parasitoid distribution around the bolt was affected by treatment. In control treatments parasitoids were most abundant at the top of the bolt and as tree retention decreased to clear-cut, parasitoids were increasingly encountered at the bottom. Parasitoid distribution may also reflect resource partitioning, as *R. xylophagorum*, *C. rufovariegatus*, and *B. tenuis* were most abundant in the top, sides, and bottom of the log surface,

respectively. Fourth instar *D. rufipennis* larvae were the instar that was parasitised (74.6%) most often. Discovery of spruce beetles by parasitoids was not affected by harvest treatment or host density, but among samples with parasitism there was a significant inverse relationship between available host density and percent parasitism. Parasitism did not differ with respect to treatment or position on log surface but beetle number was significantly correlated with parasitism in each sample.

3.2. INTRODUCTION

The spruce beetle, *Dendroctonus rufipennis* (Kirby), is one of the most destructive pests of mature spruce (*Picea* spp.) in North America (Humphreys and Safranyik 1993, Schmid and Frye 1977, Werner *et al.* 1977). Periodic, dramatic outbreaks can cause up to 95% mortality of mature trees within some stands, and can cover tens of thousands of adjoining acres of white spruce (Packee 1997; Schmid and Frye 1977). From 1974 to 1999, an estimated 3 billion board feet of lumber in British Columbia and 2 billion board feet in Alaska were lost to this beetle (Holsten *et al.* 1997). Spruce beetle outbreaks can be more important than other disturbances, including fire, in influencing the ecology of spruce forests (Veblen *et al.* 1994). Non-outbreak populations of *D. rufipennis* attack weakened and recently dead host material (Dyer and Safranyik 1977), were more common on fallen logs, as well as better brood

production per unit of bark (Safranyik 1989). The creation of large amounts of fallen host material following large-scale windfall, accumulation of logging residues and road-building favors rapid increases in local populations of *D. rufipennis*. Such events often precipitate outbreaks in adjacent stands (Reynolds and Holsten 1994; Wygant and Lejeune 1967), but this is not always the case (Safranyik 1989). It appears necessary that adjacent stands are stressed and susceptible to beetle attacks in order for an outbreak to occur (Safranyik 1989; Safranyik *et al.* 1983). Many aspects of the epidemiology of *D. rufipennis* are still poorly understood, in particular the factors that determine population growth and decline, such as the role of symbiotic phytopathogenic fungi and natural enemies.

Insect populations may be partly regulated by parasitoids, usually in a density dependent manner (LaSalle 1993; LaSalle and Gauld 1993). Parasitoids can have significant effects on bark beetle populations (Dahlsten 1982; DeLeon 1935; Linit and Stephen 1983; Moore 1972). Although there is a large suite of insect parasitoids and predators associated with *D. rufipennis*, these are best known from the Rocky Mountain area of the United States and from Alaska (Gara *et al.* 1995; Massey and Wygant 1954; McCambridge and Knight 1972; Miller *et al.* 1987, 1989; Schmid and Frye 1977). Nonetheless, the impact of parasitoids on endemic *D. rufipennis* populations and their role in *D. rufipennis* epidemiology is largely unknown (Moeck and Safranyik 1984). Spruce forests are becoming increasingly subjected to large-scale harvesting

and other anthropogenic disturbances. However, there is little empirical basis for predicting the responses of spruce beetle and its parasitoid assemblage, nor for prescribing harvesting treatments which minimize impacts on processes that determine spruce beetle-parasitoid interactions. These differences both have pest management and biodiversity conservation implications.

The increasing focus of disguising forest management strategies to better emulate natural disturbances in forest ecosystems (Attiwill 1993; Haila *et al.* 1994; Hunter 1993). This has prompted experiments to compare variable retention harvesting treatments to more traditional harvesting treatments and to natural disturbances. Much of this work is rationalized to balance economic objectives with ecological and social objectives to optimize inclusion of multiple values into forest management regimes (Jensen *et al.* 1994, Kimmins 1995). The Ecosystem Management Emulating Natural Disturbance (EMEND) Project, recently established in the boreal forest of Alberta, Canada, is one such experiment that aims to provide information required to maintaining biotic communities, spatial patterns of forest structure, and ecosystem integrity through use of innovative forest harvest and regenerative practices (Spence and Volney 1999). In this context, EMEND provided an opportunity to explore the interaction between variable retention harvesting and *D. rufipennis* as a disturbance factor in these forests. In this paper, I examine how the parasitoid assemblage associated with the *D. rufipennis* is affected by variable retention harvesting in terms of the relative abundance of parasitoid species and their

impacts on *D. rufipennis* populations. I also explore the implications for biodiversity conservation and pest management.

3.3. MATERIAL AND METHODS

3.3.1. Study Site

Work on *D. rufipennis* parasitoids was conducted at the EMEND site, situated on 1500 hectares of boreal forest land, 100 km northwest of Peace River, Alberta (Chapter 1; Volney *et al.* 1999). Of the 4 stand types included in EMEND; only conifer-dominated stands were selected for study as these are the stands most frequented by *D. rufipennis*. These stands have canopies that are 70-95% comprised of white spruce (*Picea glauca* (Moench) Voss), and the remainder comprised largely of the hardwoods, trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). Smaller amounts of white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* (L.) Mill.), and lodgepole pine (*Pinus contorta* var. *latifolia* Engelmann) were also present. Five harvesting treatments were conducted in this stand type during the winter of 1998-99, but my work was limited to three: clear-cut, 20% residual (live number of standing trees) and 50% residual as well as uncut controls. Three replicates of each treatment were included, thus spanning a total of 12 of EMEND's 10 hectare compartments. A pre-treatment survey indicated that *D. rufipennis*-infested

host material, mainly fallen logs, was present in all stands, and *D. rufipennis* populations were low (David Langor, personal communication).

3.3.2. Sampling of spruce beetle and parasitoids

Sampling of *D. rufipennis* and its parasitoids in bark commenced in 1999, immediately following application of harvesting treatments. As there was no assurance that sufficient and suitable *D. rufipennis*-infested material would be present in all treatments and replicates following harvesting, it was necessary to translocate spruce beetle-infested logs from off site into the study compartments. This approach also minimized effects of confounding factors such as tree diameter, phloem thickness and attack density, all of which are hypothesized to affect parasitism (Dahlsten 1982). In late April 1999, about 2 weeks before the start of the *D. rufipennis* flight period, 56 white spruce trees with a diameter at 1.3 m above ground of 34-40 cm (average 37.1 ± 0.2 cm) were felled in stands located about 10 kilometers south and north of the EMEND site. These trees were baited with *D. rufipennis* pheromone lures (Pherotech Ltd.) to encourage attack. In mid-June, following peak *D. rufipennis* attack but preceding parasitoid activity, 1.5 m-long bolts were cut from baited trees. Bolts chosen for use in the experiment were similar in terms of diameter (33.0 ± 3.3 cm), phloem thickness (2.8 ± 0.1 mm) and *D. rufipennis* attack density (approximately 30 entrance holes per m^2 of bark).

After translocation to study compartments, two bolts were placed end-to-end to form a 3 m-long 'log' with the long axis oriented north – south. The bark surfaces of the bolts were aligned to maintain the same orientation with respect to the ground as at the time of attack. In each of the 12 treatment or control compartments, three 'logs' were placed at least 50 m apart and 50 m from the stand edge. In most stands bolts were located in areas where there were residual trees to provide shade, although this was not possible in clear cuts.

Every two weeks spruce bark samples were removed from each log in all compartments. Because the summer was relatively cool in 1999, some individuals of *D. rufipennis* in this cohort required 2 years to complete development. Hence, sampling continued through the 2 post-treatment seasons, from 6 July to 11 September 1999 and from 10 May to 21 August 2000. Square bark samples of 100 cm^2 were cut from the top, two sides (east and west), and bottom of each log using a masonry chisel and hammer. Although it was necessary to roll the logs to sample from the underside, they were returned to their correct orientation immediately after the sample was removed. Bark samples, and any specimens remaining on the log surface after bark removal, were placed in large petri dishes, transported to the field laboratory and stored in a refrigerator for no more than 3 days before processing.

Each *D. rufipennis* individual in these samples was tallied as live, parasitised or killed by other agents. A spruce beetle larva was considered

parasitised if it had a parasitoid larva or pupa on or near it, or was paralyzed (often indicated by a scar) but with no parasitoid located nearby

3.3.3. Parasitoid Rearing and Identification

In 1998, a diet and protocol was developed to allow rearing of larval and pupal parasitoids to adulthood to facilitate identification. In 1999, parasitised spruce beetle larvae and their associated parasitoids were removed from bark samples and placed on a rearing medium developed from Robertson's (1979) spruce budworm diet by removing selected nutritive ingredients (Appendix 1). The medium was designed to maintain moisture but provide a bacteria- and fungus-free environment. About 3-4 ml of medium was poured into 10 mL plastic container fitted with a cardboard lid. Medium was made prior to use and frozen in rearing containers until needed. Generally, one parasitoid with its host was placed in each rearing container, except that in the case of superparasitism, all parasitoids from the same host were placed in one rearing container. Containers with parasitoid specimens were placed on shelves at ambient temperature and covered by dark bags to exclude light. Parasitoid rearing containers were checked daily and emerged parasitoids were placed in 75% ethanol for later identification. In October, containers with cocoons from which there was no emergence were placed in dark bags and held in cold storage (-3^0 C) to break diapause. In March 1999, parasitoids were returned to room temperature and adults began emerging after 2 weeks. Dead larvae and

live adult parasitoids were preserved in 75% ethanol for subsequent identification. Dead larvae were later identified using mandibular characteristics (Appendix 2). I identified adult parasitoid specimens using voucher specimens at the Northern Forestry Center museum in Edmonton, Alberta and identifications were verified by Gary Gibson, Henri Goulet and John Huber at the Canadian National Collection in Ottawa, Ontario.

3.3.4. Calculation of percent parasitism and development index

As only 1.6% of overall parasitism occurred on second instar *D. rufipennis* larvae, and dead second instars were often hard to locate, percent parasitism was calculated only for third larval and later instars (hereafter referred to as 'available hosts'). Thus, percent parasitism within a sample was estimated as 100(P/T), where P is the number of parasitised available hosts and T is the total number of live and dead available hosts.

Spruce beetle development was described and compared among samples and treatments with a development index. Instars were assigned the values one to seven for eggs, first, second, third, and fourth larval instars, pupae and adults, respectively. The development index was calculated as the average instar in the sample.

3.3.5. Emergence, flight and behavior

A variety of approaches were used to obtain information about spruce beetle and parasitoid emergence and flight phenology and about parasitoid oviposition. Following capture, insects were preserved in 75% ethanol pending identification.

Eight Lindgren funnel traps (Lindgren 1983) containing propylene glycol as a preservative were suspended 4 m from the ground in uncut conifer-dominated forest surrounding the EMEND site and baited with *D. rufipennis* lures containing α-pinene and frontalin (Phero Tech Inc.). Traps were checked and captured insects were removed every 2 weeks from May 11 to September 12, 1999.

In control compartments, 13 bright yellow 4x6 inch sticky traps (Moeck *et al.* 1981; from Phero Tech Inc.) were hung by wire perpendicularly to the *P. glauca* log side on felled trees and stumps baited with spruce beetle pheromone lures. Traps were deployed on July 17, 1999, after peak *D. rufipennis* flight was completed, and collected every 2 weeks until August 20, 1999. After removal, traps were wrapped in wax paper and frozen for later tally and identification of parasitoids.

Emergence traps (Langor and Raske 1987), which each sample a 100 cm^2 circular area and use propylene glycol as a preservative, were attached to spruce beetle-infested trees and emptied every 2 weeks. In 1999, 24 emergence traps were placed on each of 12 translocated logs into treatments

and these were monitored from July 4 - September 12, 1999 and from May 10 to August 8, 2000. Also in 1999, 12 emergence traps were placed on a girdled standing tree and 20 traps on a log during the second year following *D. rufipennis* attack.

Activity of *D. rufipennis* parasitoids was recorded for the surface of the translocated logs and observed during sampling in 1999 and 2000 was recorded. In addition to these casual observations, structured observation times were scheduled for all 9 translocated logs in control compartments and for 3 translocated logs in one 20% residual compartment (these compartments were chosen for regular observations because parasitoids were more frequently observed there). On each log two people made simultaneous observations for fifteen minutes once per week from 6 July to 11 September 1999 and from 10 May to 21 August 2000. to record incidence and behavioral information about the parasitoids. Observations of parasitoids were conducted on all days that samples were collected except when it was raining, in which case parasitoid observations were rescheduled for the next rain free date. Parasitoid specimens that were not identified during bark activity observations were collected using aspirators (Bioquip), identified at close range and immediately returned to the environment.

3.3.6 Statistical Analysis

All analyses were done using SPSS 10.0.5 (SPSS Inc. 1999). Composition of parasitoid assemblages was compared among treatments and among log surfaces using Chi square (χ^2) tests. First, tests were applied to data on the number of parasitised hosts in bark samples attributable to each parasitoid species. Second, as one species was a superparasitoid, χ^2 tests were also applied to data on the number of parasitoid larvae/pupae of each species found in bark samples. For all χ^2 tests, data for *R. xylophagorum* and *D. dendroctoni* were combined since there were fewer than 5 individuals from each species reared from each treatment and bark surface location.

The relationship between brood density of *D. rufipennis* and percent parasitism in each treatment and log surface for August 17, 1999 (the date when maximum parasitism was achieved) was examined graphically but could not be tested statistically. Residuals for these samples could not be normalized even by transformation and a high proportion of samples had either no parasitism or available hosts present, therefore, was not possible. Many of the cells in the contingency table had expected values less than 5, also eliminating Chi squared analyses (χ^2).

Comparison of overall percent parasitism among treatments and sample locations could not be accomplished with ANOVA as ca. 80% of samples had no parasitism and residuals could not be normalized by transformation (arcsine square root, natural log). Thus, for purposes of analyses, parasitism in these

samples was separated into two components: 1) probability of sample discovery by parasitoids and 2) conditional probability of parasitism, given discovery. Data from all treatments and log surfaces combined were subjected to regression analysis to determine if there was a relationship between density of available hosts and the proportion of samples discovered, but data points were too few to allow regression to be applied to each treatment individually. Thus, chi squared analyses (χ^2) were used to examine individually the effect of treatment and log surface on proportion of samples discovered by parasitoids. For those samples discovered by parasitoids, ANOVA (General Linear Model) was used to analyze parasitism patterns among discovered samples using treatment and log surface as the main effects and beetle density as a covariate. Data for ANOVA had normal residuals so no data transformation was required. For each sample date, the *D. rufipennis* development index (non-transformed) was compared among treatments and log surfaces using ANOVA (General Linear Model). Bonferroni pre-planned pairwise comparisons were used to detect differences between treatments and log surfaces for development index.

3.4. RESULTS

3.4.1. *D. rufipennis* Development

The first bark samples were taken on July 6, 1999, two weeks after logs were moved into the stands. At this time there was no significant difference in beetle development among treatments and most of the *D. rufipennis* progeny

were represented by 1st instar larvae (Table 3.1a). On both July 19 and August 2, development was significantly slower in control stands than in harvested stands (Table 3.1a). By August 17, most of the beetle population was represented by third larval or later instars and there was a strong effect of treatment on development. At this time spruce beetle progeny in uncut stands were significantly less developed than in all harvested stands, and development in clear cuts was significantly more advanced than in all other compartments (Table 3.1a). Since after August 17 there was untallied adult emergence from some samples and thus, it was no longer possible to calculate reliable development indices for these samples.

Beetle development pooled over all treatments was similar on all surfaces of the logs on July 6 (Table 3.1b), but by August 17, larvae on the top surfaces of logs had developed significantly faster than those at the log bottom. There was no significant interaction between treatment and log surface for August 17, 1999.

On August 17, the number of available spruce beetle hosts was similar for clear cut and 20% treatments but increased in 50% residual and control compartments, and this pattern was generally evident for all log surfaces (Fig. 3.1A). In all treatments the majority of available beetles were located in the bottom of logs (Fig. 3.1A). Clear-cut and 20% treatments had a similar proportion of overall available host in the lower surface, but the proportion of

available host in other surfaces increased in 50% residual and control compartments.

3.4.2. Parasitoid Assemblage Structure

Four species of parasitoids were found associated with *D. rufipennis*: two braconids, *Coeloides rufovariegatus* (Provancher) and *Bracon tenuis* Muesebeck & Walley, and two pteromalids, *Roptrocerus xylophagorum* (Ratzeburg) and *Dinotiscus dendroctoni* (Ashmead). Overall, only 72% of the parasitised *D. rufipennis* could be attributed to a parasitoid species as some parasitoid larvae were unidentifiable or the host was only paralyzed with no eggs or larvae found on or near it.

The highest number of parasitised available hosts occurred in control treatments and parasitism decreased as the treatment areas became less shaded (Fig. 3.1B). Of the parasitism that could be attributed to parasitoid species, 49.0%, 36.6%, 9.8% and 4.6%, respectively, were caused *C. rufovariegatus, B. tenuis, R. xylophagorum, and D. dendroctoni* (Fig. 3.2A). The proportion of spruce beetle parasitism attributable to the four parasitoid species varied significantly among treatments (χ^2 = 39.7, df=6, P < 0.001). *Coeloides rufovariegatus* was the most common parasitoid in clear cuts and controls and *B. tenuis* was the most abundant in the 20% and 50% residual treatments (Fig. 3.2A). *Roptrocerus xylophagorum* was proportionately much more abundant in clear cuts than in the other treatments (Fig. 3.2A).

All four parasitoid species are ectoparasitic and only one parasitoid was found per host for *C. rufovariegatus* and the two pteromalid species. *Bracon tenuis*, however, is a superparasitoid with an average of 2.4 (± 0.16) larvae found per host (range was 1-9). Of the total number of parasitoid larvae sampled in 1999, *C. rufovariegatus, B. tenuis, R. xylophagorum* and *D. dendroctoni* comprised 32.8%, 56.7%, 6.7% and 3.9%, respectively (see Total in Fig. 3.2A,B). Thus, the proportional representation by *B. tenuis* in the parasitoid assemblages was much higher than the proportion of parasitised hosts attributed to that species. The proportional representation by the four parasitoid species within the total parasitoid population varied significantly among treatments (χ^2 = 106.2, df=6, P< 0.001). Provided that mortality is equivalent among all parasitoid species during development, *C. rufovariegatus* will be the dominant species emerging from spruce beetle populations in clear cuts, *B. tenuis* will dominate emerging parasitoids in 20% and 50% residual treatments, and these species will be in almost equal abundance in controls (Fig. 3.2A). Proportionately, *R. xylophagorum* will be much more abundant in clear cuts than in other treatments.

The distribution of parasitism events around the log surface was congruent with the distribution of available hosts (Fig. 3.1A,B) in clear cut and 20% residual treatments; however, as the percent residual increased, parasitism events occurred primarily on the sides and tops of logs (Fig. 3.1B). Individual parasitoid species were associated with various parts of the logs

during oviposition (χ^2 = 71.1, df=6, P < 0.001). *Roptrocerus xylophagorum* was the dominant parasitoid attacking tops of logs, despite the fact that it was one of the least abundant parasitoids; *C. rufovariegatus* was found predominantly on the sides of logs, and caused over 70% of the parasitism events; and *B. tenuis* were most common on the bottoms of logs (Table 3.2). A similar pattern was evident for the number of parasitoid progeny produced on different log surfaces (χ^2 = 131.7, df=6, P < 0.001) (Fig. 3.2B).

3.3.3 Treatment effects on parasitism

Parasitism of *D. rufipennis* was first noted on July 19, 1999 in the three harvesting treatments and on August 7 in the controls (Fig. 3.3), and most parasitism had accrued by the August 17 sample date as no new cases of parasitism were encountered after this date (note data for parasitism and number of parasitised hosts in Fig. 3.3). Emergence of new brood adults had commenced in all treatments by August 29 (note decline in number of available beetles from Aug. 17 to Aug. 29 (Fig. 3.3)), but these adults were not tallied. Thus percent parasitism could be estimated only for those samples taken on August 17. Of the 144 samples taken on this date, 77 contained available hosts and could be analyzed. Parasitism was sub-divided into two components for examination. First, the chance of sample discovery by parasitoids was compared among treatments using the 77 samples containing available hosts.

Then conditional probability of parasitism given discovery was compared among treatments using the 35 samples that sustained parasitism.

Overall, only 45% of samples with available beetles were discovered by parasitoids and the chances of sample discovery did not vary significantly among harvesting treatments (Table 3.3a; χ^2 =0.27, df=3, P = 0.970) or around the circumference of logs (Table 3.3b; χ^2 =2.49, df=3, P = 0.477). Regression analysis showed that there was no relationship between density of available hosts and probability of discovery (R^2 = 0.003, P = 0.670).

Within samples containing parasitism there was a significant inverse relationship between density of available hosts and percent parasitism (R^2 = 0.896, P < 0.001), and for this reason density of available hosts was included as a covariate in the analysis of variance to assess treatment effects on percent parasitism in discovered samples. Although percent parasitism appear to vary from 34.5% to 54.5% in different treatments (Table 3.4a) this variation was not significant ($F_{3, 31}$ = 0.67, P = 0.581). Observed percent parasitism was highest on hosts in the top surface (74%) and lowest for those in the bottom surface (32%), but overall this was not significant (Table 3.4b, $F_{3, 31}$ = 0.73, P = 0.546). As the earlier regression of percent parasitism and available host density suggested, available beetle density was a significant factor determining parasitism proportion in each sample (Table 3.4, $F_{3, 31}$ = 22.20, P < 0.001), but the interactions between host density and the main effects were insignificant.

3.4.4 Parasitoid Phenology and Behavior

Flight and oviposition of parasitoids peaked in early August (Fig. 3.4), when spruce beetle progeny were mainly third and fourth larval instars (Fig. 3.3), and number of parasitoid larvae in bark samples peaked in mid-August. The fourth larval instar was the most severely affected by each parasitoid species (Table 3.5), and overall this instar experienced almost 75% of the total parasitism events. *Coeloides rufovariegatus* was the most abundantly captured and observed species, it's flight period extended from early July to mid-September (Fig. 3.4A). The other species appeared to have shorter flight periods, extending from mid-to-late July to mid-August. *Bracon tenuis* was rarely caught in traps, although it was relatively abundant in bark samples. After mid-August, there was little accrual of parasitism as indicated by bark samples. Thus, parasitoids flying in late August and September were probably those finished reproducing or the next generation of parasitoid adults that had completed development and emerged. Although some parasitoids did emerge in August and September 1999, these were not tallied, but comparison of the average number of parasitoids in samples from August 17, 1999 to May 10, 2000 suggests that as many as 75% of parasitoids emerged before winter (Table. 3.6). There was no evidence that these emerged parasitoids reproduced on spruce beetle hosts in the year of emergence. Some larvae of all species overwintered in the logs. No parasitoids emerged from sample logs during winter and spring until mid June 2000.

Only *C. rufovariegatus* was observed sufficiently often to provide reliable data on behavior. It appears that some mating occurs on the bark surface (observed once). On one occasion, a mating swarm of *C. rufovariegatus* was observed on the bark surface of a spruce log. The swarm had approximately 20 males tightly grouped around 1 female. The group of parasitoids flew away after a brief observation period.

During oviposition, females antennated over an area on the bark surface, alternately touching their antennal tips to the bark surface. An area as small as 5 cm^2 was communally shared with up to 5 other antennating *C. rufovariegatus* females without evidence of aggression or territoriality. When a female determined that a oviposition site was suitable, she probed the bark several times with a vertically oriented ovipositor, apparently to determine exact placement. Then, she placed her ovipositor at right angles to the bark surface and drilled. The female's abdomen pulsated as the ovipositor entered the bark, a process that may last 3-6 minutes, depending on the bark and phloem thickness. After a female of *C. rufovariegatus* had inserted her ovipositor into the bark, the ovipositor was removed with the same pulsating abdomen motion and about the same time as required for ovipositor insertion. Before the ovipositor was entirely removed from the bark it could be oriented to a different angle and inserted into the bark a second time. This procedure was done without the female assuming another body position. After ovipositor insertion and removal, the female then turned her body approximately 90° (clockwise

usually), relocated the oviposition site with her ovipositor and inserted the ovipositor into the bark again, using the same pulsating motion of the abdomen. This second drilling took about the same time as the initial bark entrance and removal. After this ovipositor insertion and removal a female cleaned her ovipositor with her hind legs while remaining in the same location. After cleaning the female remained motionless for 3 minutes before repeating the oviposition site location procedures a second time. This highly stereotyped procedure was observed in the field five times.

There was evidence of interference competition between *C. rufovariegatus* and *D. dendroctoni*. When *D. dendroctoni* encroached on a *C. rufovariegatus* female, the *C. rufovariegatus* defender either chased the invader away or rammed it until it was dislodged from the bark surface. Females of *C. rufovariegatus* interrupted site selection or oviposition behavior to chase off *D. dendroctoni* in both encounters observed.

3.5 DISCUSSION

3.5.1. Spruce beetle development and host availability

The life cycle of the spruce beetle varies from 1-3 years, depending on temperature conditions, but the 2-year cycle is most common in western Canada (Safranyik 1989). Rate of larval development, and hence the length of the life cycle, is a function of phloem temperature, which is strongly influenced by solar radiation (Werner and Holsten 1983, 1985; Hansen *et al.* 2001a). Thus,

it is common that different parts of the same tree or log may have univoltine or bivoltine beetles, depending on exposure to direct solar radiation (Safranyik 1989). Although spruce beetle development was at about the same stage on all log surfaces and in all sample logs at the time that they were translocated to treatment and control compartments, differences in exposure to sunlight resulted in differences in development rate. By August 17, beetles had developed significantly faster in clear cuts and in the top surfaces of logs. An unestimated proportion of the beetle population completed development to adulthood within one year, and it is reasonable to expect that the proportion of univoltine beetles increased with the amount of sun-exposure. Safranyik *et al.* (1983) reported 66% of beetles in logging residual and 22% of beetles in windfall had a 1-year life cycle. As spruce beetle epidemiology appears to be in part influenced by proportion of beetles which are univoltine (Safranyik et al. 1983; Reynolds and Holsten 1994), forest managers must be aware of the potential consequences of management activities in spruce forests which increased availability of suitable host material and rate of beetle development. A temperature-based model to predict proportion of univoltine spruce beetles may help identify risk and aid management decisions (Hansen *et al.* 2001b).

The density of available spruce beetle hosts available for parasitism on August 17 was likely largely influenced by the original density of eggs laid, development rate and mortality by other agents. Although the relative importance of these three factors (and perhaps others) could not be separated

in this study, the end result was that the lowest density of available hosts was available in clear cut and 20% residual compartments, and within these compartments almost all available hosts were located in the lower surface of logs, thereby limiting the action of parasitoids to these surfaces. As the amount of stand residual, and hence shading, increased, so did the overall density of available hosts, and increasingly more hosts were available on the sides and tops of logs, providing more opportunity for parasitoids to distribute themselves around the circumference of logs.

3.5.2 Parasitoid assemblage structure and biology

Except for *B. tenuis*, the parasitoid species found attacking the *D. rufipennis* in this study have also been reported from *D. rufipennis* in Alaska and Colorado (Bushing 1965; DeLeon 1935; Gara *et al.* 1995; Krombein 1958; Massey and Wygant 1954; McCambridge and Knight 1972; Peck 1963). Gara *et al.* (1995) noted that *Bracon* sp. was reared in association with *D. rufipennis* in Alaska, but the individuals were not identified to species. McCambridge and Knight (1972) report that parasitism in Colorado was mostly by *C. rufovariegatus* and resulted in 0.4 – 6.1% *D. rufipennis* mortality. Also in Colorado, Massey and Wygant (1954) reported that *C. rufovariegatus* was the most important parasitoid of spruce beetle larvae, but *D. dendroctoni* and *R. xylophagorum* were also effective parasitoids. In Alaska, Gara *et al.* (1995) found *R. xylophagorum* to be the most abundant spruce beetle parasitoid,

followed by *D. dendroctoni* and *C. rufovariegatus*. Although other authors (e.g., Gara *et al.* 1995) have reported many other parasitoid species associated with *D. rufipennis*, in all cases parasitoids were reared from bolts infested by *D. rufipennis* and other scolytid species. Thus, specific host-parasitoid relationships could not be ascertained. The current study is the first to clearly establish specific spruce beetle-parasitoid relationships.

In 1999, *C. rufovariegatus* was the dominant parasitoid in terms of impact on *D. rufipennis*, and accounted for 49.0% of the total recognizable parasitism. This species had the longest flight period and was the most aggressive parasitoid on the bark surface, which may contribute to its success. However, assuming similar survival among larvae of all parasitoid species, the superparasitoid, *B. tenuis*, was the most abundant parasitoid at emergence; in the first post-treatment parasitoid generation 56.7% of parasitoid larvae found were of this species. It may be, therefore, that the relative abundance and impact of the four parasitoid species will change over time at the EMEND site, but this depends very much on relative fecundity, survival and propensity to attack other host species (all are bark beetle generalists and some even attack other families of wood-boring beetles) (Dahlsten 1982).

The high variability of proportional abundance of the four parasitoid species around the circumference of logs may reflect active choices for oviposition sites rather than differential mortality, as mortality of parasitoids was very low (no cases of mortality were observed). In terms of overall parasitism, a

null hypothesis might reasonably predict that spatial patterns in percent parasitism would be congruent with the distribution of available hosts. Specifically, this hypothesis would then predict that control compartments and the bottom log surfaces should be best for parasitoids. Parasitism was indeed highest in control compartments, but in these compartments the strongly inverse relationship between host density and percent parasitism suggests that hosts in bottoms of logs may be underutilized, perhaps because the microhabitat is not ideal for parasitoids. Alternatively, this pattern of host utilization may simply be an outcome of parasitoid landing and host searching patterns. Parasitoids were observed to land on the top surfaces of logs initially and commence searching and ovipositing there, eventually moving down the sides and to the bottoms. By the time parasitoids reached the bottom of the logs, they likely had fewer eggs to lay but there was greater host availability, resulting in under utilization and low percent parasitism. However, parasitism patterns are best understood when the activities of different parasitoid species are examined individually, both in terms of percent parasitism and number of parasitism events.

Although *C. rufovariegatus* caused over 70% of the total parasitism on the sides of logs, the number of parasitism events caused by this species was the same on sides and bottoms. Thus, there is no compelling evidence to suggest that *C. rufovariegatus* was most common on log sides over bottoms; however, the relative rarity of this parasitoid in the tops of logs suggests that

this is not a chosen oviposition location or that females are not as efficient at locating hosts when host density is very low. All other three parasitoid species showed strong affinity for the bottom surfaces of logs, as indicated by number of parasitism events. *Bracon tenuis* exhibited the strongest correlation with log bottoms, accounting for 54% of total parasitism events on that surface and 75% of all parasitism events by that species. Additionally, *R. xylophagorum* was proportionately most abundant in the tops of logs and clear-cut areas, suggesting that this species chooses sun-exposed habitats. There is little information available on the best microhabitat for bark beetle parasitoids; however, there is evidence that due to physical limitations of ovipositor length, parasitoid success and spatial distribution on trees may be limited by bark thickness (Ball and Dahlsten 1973; Dahlsten and Stephen 1974). However, some parasitoids with short ovipositors, e.g. *R. xylophagorum*, are able to enter bark beetle galleries to seek hosts and are not limited to oviposition through the bark (Berisford *et al.* 1970; Dahlsten and Bushing 1970; Reid 1957).

The flight periods of all four species overlap with the occurrence of third larval and later instars of *D. rufipennis*. As parasitoid larvae must develop on one host there are advantages (e.g., survival & fecundity of the F1 generation) to attacking the largest host, and synchrony between availability of the largest host instars and peak flight of parasitoids is a general pattern (Camors and Payne 1973; Dahlsten 1982; Dixon and Payne 1979; Edson 1978; Stephen and Dahlsten 1976). Parasitoids *C. rufovariegatus* and *B. tenuis* began emerging in

late August but emergence phenology was not monitored. It is not known if these emerged individuals have an obligatory diapause, but the fact that no additional parasitism accrued on spruce beetle larvae after August 17 suggests that they are not actively seeking new hosts and may simply feed on nectar (Kevan *et al.* 1993; Syme 1975) and overwinter. Adults may be long-lived as females of *Coeloides brunneri* Viereck survived an average of 32.9 days and males 22.2 days on a honey diet at room temperature (Ryan and Rudinsky 1962).

C. rufovariegatus, R. xylophagorum and *D. dendroctoni* have broad host ranges (Dahlsten 1982), including many other bark beetle species. Thus the impact of these species on spruce beetle may be influenced by the abundance of other bark beetles in the same logs and stands.

3.5.3 Parasitoid responses to treatments

Although there is biological utility in sub-dividing parasitism to first examine chances of patch discovery and then parasitism within discovered patches (Kreuss and Tscharntke 1994; Morrison and Strong 1981; Roland and Taylor 1995), insufficient information is available to adequately define the spatial and temporal parameters of a patch from the functional viewpoint of spruce beetle parasitoids. In this study, the 100 cm^2 circular bark samples were used as a rough proxy of patch, without knowing if parasitoids respond to host density at this scale. Nonetheless, the lack of treatment effects on probability of

discovery by parasitoids, and the lack of a relationship between available host density and chances of discovery (all treatments combined), suggests that *D. rufipennis* parasitoids use cues other than host density to select oviposition sites. For example, the large amount of logging slash present immediately following harvest may attract parasitoids (Dahlsten 1982). Also, although all four parasitoid species were present in all treatments, the degree of sun-exposure seems to have influenced the relative abundance of the species, and hence the chances of patch discovery by individual parasitoid species. Generally, it is believed that parasitoids are initially attracted to the host habitat and then to the host, which they then choose to accept or reject. (Doutt 1965; Richerson and Borden 1972a). Thus, sample discovery for each treatment depends on a complicated set of decisions by the parasitoids and much behavioral work is needed to ascertain how parasitoids select patches and hosts.

Parameters that determine whether parasitoids oviposit and the amount of reproductive effort invested in a host patch are also little understood (Waage and Greathead 1986; Richerson and Borden 1972b). Studies conducted on *Coeloides* spp. indicated that parasitoids which oviposit through bark may use cues like infrared radiation from host muscle or, less likely, sound or vibration from host feeding or host odor (DeLeon 1935; Richerson and Borden 1971, 1972a, b; Ryan and Rudinsky 1962). My observations suggest that antennae are an important tool to help *C. rufovariegatus* identify oviposition sites.

The significant inverse relationship between beetle density and percent parasitism proportion largely reflects the pattern in 50% residual and control compartments as parasitism events in these compartments comprised 71.8% of the total number of events. This relationship suggests that even though all treatments may have an equal chance of discovery, a beetle larva feeding in a high density patch is less likely to be parasitised than if feeding in an area where density is low. Thus, there may be a significant benefit to host clumping, as has been demonstrated in other host-parasitoid systems (Brown and Cameron 1979; Burnett 1958; Hirose *et al.* 1976; Morrison *et al.* 1980; Reeks 1953).

Although there was no overall impact of harvesting treatment on percent parasitism in discovered samples, there was some evidence of treatment effects on the distribution of parasitism around the circumference of logs. In control stands, which represent the usual stand conditions for *D. rufipennis* populations, parasitism was concentrated on the top and sides of logs although the densities of available beetles were highest on bottoms. It may be that in control stands the bottoms of logs are too shaded and cool for optimum parasitoid development. Thus, concentration of *D. rufipennis* oviposition on lower surfaces of logs may be a parasitoid-avoidance mechanism. However, as stands are increasingly opened up by harvesting, parasitoids increasingly utilize hosts in the bottom surface of each bolt. These results suggest that partial harvesting of stands may be detrimental to *D. rufipennis* as the increased

exposure of breeding material makes exposed surfaces less suitable for beetle development and survival and also makes the lower surface more susceptible to parasitism. However, these disadvantages may be partially offset by the faster development of *D. rufipennis* and the fact that a higher proportion of beetles are univoltine than in more shaded stands (Safranyik *et al.* 1983).

3.6. REFERENCES

Attiwill, P.M. 1993. The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manag.* **63**: 247 – 300.

Ball, J.C., D.L Dahlsten. 1973. Hymenopterous parasites of *Ips paraconfusus* (Coleoptera: Scolytidae) larvae and their contributed mortality. I. Influence of host tree and tree diameter on parasitization. *Can. Entomol.* **105:** 1453 – 1464.

Berisford, C.W., H.M. Kuhlman, R.L. Pienkowski. 1970. Notes on the biologies of Hymenopterous parasites of *Ips* spp. bark beetles in Virginia (Coleoptera: Scolytidae) Can. Entomol. 103: 235-239.

Brown, M.W. and E.A. Cameron. 1979. Effects of disparlure and egg mass size on parasitism by the gypsy moth egg parasite, *Ooencyrtus kuwanai*. *Env. Entomol.* **8**: 77-80.

Burnett, T. 1958. Dispersal of an insect parasite over a small plot. *Can. Entomol.* **90**: 279-283.

Bushing, R.W. 1965. A synoptic list of the parasites of Scolytidae (Coleoptera) in North America north of Mexico. *Can. Entomol.* **97(5)**:449 – 492.

Camors F.B., Jr. and T.L. Payne. 1973. Sequence of arrival of entomophagous insects to trees infested with the southern pine beetle. *Env. Entomol.* **2:** 267 – 270.

Dahlsten, D.L. 1982. Relationships between bark beetles and their natural enemies. Pp. 140-182 *In:* Bark Beetles in North America Conifers, (J.B. Mitton and K.B. Sturgeon, Eds.). Univ. of Texas, Austin.

Dahlsten, D.L. and R.W. Bushing. 1970. Insect parasites of the western pine beetle. pp. 113-118 *In:* Studies on the population dynamics of the western pine beetle, *Dendroctonus brevicomis* Le Conte (Coleoptera: Scolytidae) (R.W. Stark and D.L. Dahlsten, Eds.). University of California, Div. of Agric. Sci.

Dahlsten, D.L. and F.M. Stephen. 1974. Natural enemies and insect associates of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in sugar pine. *Can Entomol.* **106:** 1211 – 1217.

DeLeon, D. 1935. The biology of *Coeloides dendroctoni* Cushman (Hymenoptera- Braconidae) an important parasite of the Mountain Pine beetle (Dendroctonus *monticolae* Hopk.). *Ann. Entomol. Soc. Am.* **28**(4): 411-424.

Dixon, W.N. and T.L. Payne. 1979. Aggregation of *Thanasimus dubius* on trees under mass-attack by the southern pine beetle. *Env. Entomol.* **8:** 178 – 181.

Doutt, R.L. 1965. Biological characteristics of entomophagous adults, pp.145-167. *In*: Biological control of insect pests and weeds (P. DeBach, Ed.), Reinhold Pub. Co., New York. pp. 145-167.

Dyer, E.D.A. and L. Safranyik. 1977. Assessment of pheromone –baited trees on a spruce beetle population (Coleoptera: Scolytidae). *Can. Entomol.* **109**: 77-80.

Edson, L.J. 1978. Host colonization and the arrival sequence of the mountain pine beetle and its insectan associates. Ph.D. Thesis, Univ. of California, Berkeley. 196pp.

Gara, R.I., R.A. Werner, M.C. Whitmore and E.H. Holsten. 1995. Arthropod associates on the spruce beetle *Dendroctonus rufipennis* (Kirby) (Col., Scolytidae) in spruce stands of south central and interior Alaska. *J. Appl. Entomol.* **119**: 585-590.

Haila, Y., I.K. Hanski, J. Niemela, P. Punttila, S. Raivio and H. Tukia. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. *Ann. Zool. Fennici* **31**: 187 – 202.

Hansen, M.E., B.J. Bentz and D.L. Turner. 2001a. Physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). *Can. Ent.* **133**:805-817.

Hansen, M.E., B.J. Bentz and D.L. Turner. 2001b. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Can. Ent.* **133**:827-841.

Hirose, Y., H. Kimoto and K. Hiehata. 1976. The effect of host aggregation on parasitism by *Trichogramma papilionis* Nagarkatti (Hymenoptera:

Trichogrammatidae), an egg parasite of *Papilio xuthus* Linne (Lepidoptera: Papilionidae). *Appl. Entomol. Zool.* **11**: 116-125.

Holsten, E.H., R.W. Their, A.S. Munson and K.E. Gibson. 1997. The Spruce Beetle. USDA Forest Service, Forest Insect and Disease Leaflet No. 127. 8pp.

Humphreys, N. and L. Safranyik. 1993. Spruce Beetle. Canada- B.C. Partnership Agreement FRDA II: For. Pest Leaf. 13. 7pp.

Hunter, M.L. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biol. Conserv.* **65**: 115 – 120.

Jensen, M.E., P.S. Bourgeron. 1994. Volume II: Ecosystem management: principles and applications. U.S.D.A., Pac. NW, Res. Stn., Gen. Tech. Rep. 318., 376 pp.

Kevan, P.G., E.A. Tikhenev and M. Usui. 1993. Insects and plants in the pollination ecology of the boreal zone. *Ecol. Res.* **8**: 247-267.

Kimmins, J.P. 1995. Sustainable development in Canadian forestry in the face of changing paradigms. *For. Chron.* **71**(1): 33-40.

Kreuss, A. and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. *Science.* **264,** 1581 – 1584.

Krombein, K.V. 1958. Hymenoptera of America north of Mexico, synoptic catalog. *Agric. Monogr.* U.S.D.A., 1st Suppl. 2, 305pp.

Langor D.W. and A.G. Raske. 1987. Emergence, host attack and overwintering of the eastern larch beetle, *Dendroctonus simplex* LeConte

(Coleoptera: Scolytidae), in Newfoundland. *Can. Entomol.* **119:** 985 – 992.

LaSalle, J. 1993. Parasitic Hymenoptera, Biological Control and Biodiversity. *In*: Hymenoptera and Biodiversity (LaSalle, J. and I.D. Gauld, Eds.), CAB International, Wallingford, pp. 197-215.

LaSalle, J. and I.D. Gauld. 1993. Hymenoptera: Their Diversity and Their Impact on the Diversity of Other Organisms. *In*: Hymenoptera and Biodiversity (LaSalle, J. and I.D. Gauld, Eds.), CAB International, Wallingford, pp. 1-26.

Lindgren, B.S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). *Can Entomol.* **115:** 299-302.

Linit, M.J. and F.M. Stephen. 1983. Parasite and predator component of within-tree southern pine beetle (Coleoptera: Scolytidae) mortality. *Can. Entomol.* **115**: 679-688.

Massey, C.L. and N.D. Wygant. 1954. Biology and control of the Engelmann spruce beetle in Colorado. USDA For. Serv. Circular No. 944, 35pp.

McCambridge, W.F. and F.B. Knight. 1972. Factors affecting spruce beetle during a small outbreak. *Ecology* **53**(5): 830-839.

Miller, M.C., J.C. Moser, M. McGregor, J.C. McGregoire, M. Basier, D.K. Dahlsten and R.A. Werner. 1987. The potential for biological control of native north American *Dendroctonus* beetles (Coleoptera: Scolytidae). Forum section, *Ann. Entomol. Soc. Amer.* **80**: 417-428.

Miller, M.C., M. McGregor, D.L. Dahlsten, M.C. Whitmore, J.C. Gregoire, I-X Zhou, R.A. Werner, Y.S. Chow, D. Cibrian Tovar, R. Campos Balanos and Z. Mendel. 1989. Responses to insect associates of allied species to *Dendroctonus* and *Ips* (Coleoptera: Scolytidae) aggregation pheromone: a search for biological control agents. *In*: Potential for biological control of *Dendroctonus* and *Ips* bark beetles (D.L. Kulhavy, M.C. Miller; Eds.). Nacagdoches; Stephen F. Austin University.

Moeck, H.A., D.L. Wood, K.Q. Lindahl, Jr. 1981. Host selection behavior of bark beetles(Coleoptera: Scolytidae) attacking *Pinus ponderosae*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. *J. Chem. Ecol.* **7:** 49-83.

Moeck, H.A. and L. Safranyik. 1984. Assessment of predator and parasitoid control of bark beetles. Pacific For. Res. Center. Inf. Rep. BC- X- 248.

Moore, G.E. 1972. Southern pine beetle mortality in North Carolina caused by parasites and predators. *Env. Entomol.* **1**(1): 58-65.

Morrison, G., W.J. Lewis and D.A. Nordlund. 1980. Spatial differences in *Heliothis zea* egg density and the intensity of parasitism by *Trichogramma* spp.: an experimental analysis. *Env. Entomol.* **9**: 149-152.

Morrison, G. and D.R. Strong. 1981. Spatial variation in egg density and the intensity of parasitism in a neotropic chrysomelid (*Cephaloleia consanguinea*). *Ecol. Entomol.* **6**: 55-61.

Packee, E.C. 1997. Restoring spruce beetle- impacted forests in Alaska. *Agroborealis*. **29**(1): 18-24.

Peck, O. 1963. A catalog of the nearctic Chalcidoidea (Insecta: Hymenoptera). *Can. Entomol. Suppl.* **30**, 1092 pp.

Reeks, W.A. 1953. The establishment of introduced parasites of the European spruce sawfly (*Diprion hercyniae* Htg.) (Hymenoptera: Diprionidae) in the Maritime Provinces. *Can. J. Agric. Sci.* **33**: 405-429.

Reid, R.W. 1957. The bark beetle complex associated with lodgepole pine slash in Alberta. Part II. Notes on the biologies of several Hymenopterous parasites. *Can. Entomol.* **90:** 464-468.

Reynolds, K.M. and E.H. Holsten. 1994. Relative importance of risk factors for spruce beetle outbreaks. *Can. J. For. Entomol.* **24**: 2089 -2095.

Richerson, J.V. and J.H. Borden. 1971. Sound and vibration are not obligatory host finding stimuli for the bark beetle parasite, *Coeloides brunneri* (Hymenoptera: Braconidae). *Entomophaga* **16**(1): 95 – 99.

Richerson, J.V. and J.H. Borden. 1972a. Host finding behavior of *Coeloides brunneri* (Hymenoptera: Braconidae). *Can. Entomol.* **104**: 1235 - 1250.

Richerson, J.V. and J.H. Borden. 1972b. Host finding by heat perception in *Coeloides brunneri* (Hymenoptera: Braconidae). *Can. Entomol.* **104**: 1877 -1881.

Robertson, J. Rearing the Western Spruce Budworm. USDA Forest Service, Oct. 1979. 10pp.

Roland, J. and P.D. Taylor. 1995. Herbivore and natural enemy interactions in fragmented continuous forests. *In*: Population dynamics: New approaches and synthesis (Cappuccino, N. and P.W. Price, Eds.) Academic, San Diego, pp. 195 – 208.

Ryan, R.B. and J. A. Rudinsky. 1962. Biology and habits of the Douglas- Fir beetle parasite, *Coeloides brunneri* Viereck (Hymenoptera: Braconidae), in Western Oregon. *Can. Entomol.* **94**: 748-763.

Safranyik, L., D.M. Shrimpton and H.S. Whitney. 1983. The role of host-pest interaction in population dynamics on *Dendroctonus rufipennis* (Kirby) (Coleoptera: Scolytidae). *In*: The Role of the Host in the Population Dynamics of Forest Insects (A.S. Isaev, Ed.). Proceedings of International Union of Forest Research Organizations/Man and Biosphere Symposium, Irkutsk, USSR, August 1981.

Safranyik, L. 1989. The population biology of the spruce beetle in western Canada and implications for management. *In:* Integrated Control of Scolytid Bark Beetles (T.L. Payne and H. Saarenmaa, Eds.). Virginia Polytechnic and State University, Blacksburg, Virginia. pp. 3-23

Schmid, J.M. and R.H. Frye. 1977. Spruce beetle in the Rockies. USDA Forest Service, Rocky Mountain Forest and Range Experimental Station. Gen. Tech. Rept. RM-49, 38 pp.

Spence, J.R. and W.J. Volney. 1999. EMEND- Ecosystem management emulating natural disturbance. Sustainable For. Manag. Network Proj. Rept. 1999-14.

S.P.S.S. version 10.0.5. 1999. S.P.S.S. Incorporated.

Stephen, F.M. and D.L Dahlsten. 1976. The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. *Can. Entomol.* **108:** 283 – 304.

Syme, P.D. 1975. The effects of flowers on the longevity and fecundity of two native parasites of the European pine shoot moth in Ontario. *Environ. Entomol.* **4:** 314-318.

Veblen, T.T., K.S. Hadley, E.M. Nel, T. Kitzberger, M. Reed and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *J. Ecol.* **82:**125-35.

Volney, W.J.A., Spence, J.R., Weber, M.G., Langor, D.W., Mallet, K.I., Johnson, J.D., Edwards, I.K., Hillman, G.R. and Kishchuk, B.E. 1999. Assessing components of ecosystem integrity in the EMEND experiment. Pages 244-249 *in* T.S. Veeman *et al.*, eds. Science and practice: sustaining the boreal forest, SFM network, 14-17 Feb.1999, Edmonton.

Waage, J. and D. Greathead. 1986. Preface. *In*: Insect Parasitoids (Waage, J. and D. Greathead, eds.) Academic Press, London, pp. xi-xii.

Werner, R.A., B.H. Baker and P.A. Push. 1977. The spruce beetle in white spruce forests of Alaska. U.S.D.A For. Serv. Gen. Tech. Rept. PNW-61. 13pp.

Werner, R.A. and E.H. Holsten. 1983. Effect of phloem temperature on development of spruce beetles in Alaska. *In*: The role of the host in the population dynamics of forest insects (L. Safranyik, Ed.). Proceedings of an IUFRO conference, Banff Centre, September 4-7, 1983.

Werner, R.A., E.H. Holsten. 1985. Factors influencing generation times of spruce beetles in Alaska. Can. J. For. Res. **15**: 438-43.

Wygant, N.D. and R.R. Lejeune. 1967. Engelmann spruce beetle *Dendroctonus obesus* (Mann.). *In*: Important Forest Insects and diseases of mutual concern to Canada, the United States and Mexico. Canada Dept. For. Rural Development Publ. 1180.

Table 3.1. Average development index (± SE) of *Dendroctonus rufipennis* in: A) harvesting treatments and; B) different log surfaces pooled across treatments in 1999. In columns with significant main effects as determined by ANOVA (α=0.05), cells with the same letter indicate no significant difference (Bonferroni tests).

A)

Treatment	July 6	July 19	August 2	August 17
Clear cut	1.20 ± 0.13	2.12 ± 0.19^{b}	3.78 ± 0.14^{b}	5.11 ± 0.21^{c}
20% residual	1.00 ± 0.00	2.24 ± 0.12^{b}	3.58 ± 0.12^{b}	4.38 ± 0.23^{b}
50% residual	1.00 ± 0.00	2.24 ± 0.14^{b}	3.43 ± 0.11^{b}	4.37 ± 0.19^{b}
Control	1.01 ± 0.01	1.66 ± 0.09^{a}	2.97 ± 0.08^{a}	3.91 ± 0.09^{a}
	$F_{3,46}$=2.46, P=0.080	$F_{3,83}$=4.74, P=0.005	$F_{3,71}$=8.34, P<0.001	$F_{3,61}$=8.05, P<0.000

B)

Log Surface	July 6	July 19	August 2	August 17
Top	1.00 ± 0.00	1.72 ± 0.17	2.90 ± 0.18	4.70 ± 0.37^{b}
East	1.01 ± 0.01	2.07 ± 0.16	3.47 ± 0.12	4.19 ± 0.18^{a}
Bottom	1.03 ± 0.03	2.02 ± 0.12	3.34 ± 0.11	4.27 ± 0.14^{a}
West	1.11 ± 0.09	2.19 ± 0.12	3.26 ± 0.13	4.10 ± 0.12^{a}
	$F_{3,46}$=1.68, P=0.191	$F_{3,83}$=1.20, P=0.315	$F_{3,71}$=1.24, P=0.303	$F_{3,61}$=4.74, P=0.005

Table 3.2. Numbers (%) of spruce beetle progeny attacked by each of four parasitoid species for each log surface.

Parasitoid Species	Log Surfaces				Total
	Top	East	Bottom	West	
Coeloides rufovariegatus	6 (4.0%)	47 (31.3%)	48 (32.0%)	49 (32.7%)	150
Bracon tenuis	3 (2.7%)	13 (11.6%)	84 (75.0%)	12 (10.7%)	112
Roptrocerus xylophagorum	7 (23.3%)	3 (10.0%)	14 (46.7%)	6 (20.0%)	30
Dinotiscus dendroctoni	2 (14.3%)	2 (14.3%)	9 (64.3%)	1 (7.1%)	14
Total	18 (5.9%)	65 (21.2%)	155 (50.7%)	68 (22.2%)	306 (100.0%)

Table 3.3. Number of 100 cm^2 bark samples containing available *D. rufipennis* hosts discovered by parasitoids in each a) treatment and b) log surface.

A)

Treatment	Discovered	Not Discovered	Total
Clear cut	5	7	12
20% residual	4	6	10
50% residual	11	12	23
Control	15	17	32
Total	35	42	77

B)

Log Surface	Discovered	Not Discovered	Total
Top	6	3	9
East	8	10	18
Bottom	13	21	34
West	8	8	16
Total	35	42	77

Table 3.4. Mean parasitism proportion (± SE) for available beetles contained in discovered log samples in each a) treatment ($F_{3, 31}$= 0.667, P = 0.581) and b) log surface ($F_{3, 31}$ = 0.727, P = 0.546). Beetle density was used as a covariate in this Univariate GLM ($F_{1, 33}$ = 22.202, P < 0.001).

A)

Treatment	Mean % (± SE)
Clear cut	43.2 ± 14.9
20% residual	34.5 ± 22.4
50% residual	45.5 ± 11.3
Control	54.5 ± 7.4
Total	47.8 ± 5.6

B)

Log Surface	Mean % (± SE)
Top	74.3 ± 12.0
East	48.6 ± 9.8
Bottom	32.1 ± 9.1
West	52.5 ± 11.3
Total	47.8 ± 5.6

Table 3.5. Numbers (%) of spruce beetle progeny attacked by each of four parasitoid species.

Parasitoid Species	Beetle Instar or Stage					
	Second Instar	Third Instar	Fourth Instar	Pupa	Teneral	Total
Unknown	4 (3.6%)	32 (28.6%)	74 (66.1%)	1 (0.9%)	1 (0.9%)	112
Coeloides rufovariegatus	1 (1.0%)	23 (23.7%)	73 (75.3%)	0 (0.0%)	0 (0.0%)	97
Bracon tenuis	1 (1.2%)	15 (18.3%)	66 (80.5%)	0 (0.0%)	0 (0.0%)	82
Roptrocerus xylophagorum	1 (4.3%)	2 (8.7%)	18 (78.3%)	2 (8.7%)	0 (0.0%)	23
Dinotiscus dendroctoni	0 (0.0%)	0 (0.0%)	13 (100%)	0 (0.0%)	0 (0.0%)	13
Total	7 (2.1%)	72 (22.0%)	244 (74.6%)	3 (0.9%)	1 (0.3%)	327 (100.0%)

Table 3.6. Number of parasitoid larvae and cocoons collected and reared from all 100 cm^2 bark samples in treatments and controls for 4 sample dates.

	Treatment				
Sample Date	**Clear Cut**	**20% Residual**	**50% Residual**	**Control**	**Total**
August 17, 1999	19	7	33	60	119
August 29, 1999	11	13	20	32	76
September 11, 1999	10	2	14	17	43
May 10, 2000	1	5	3	21	30

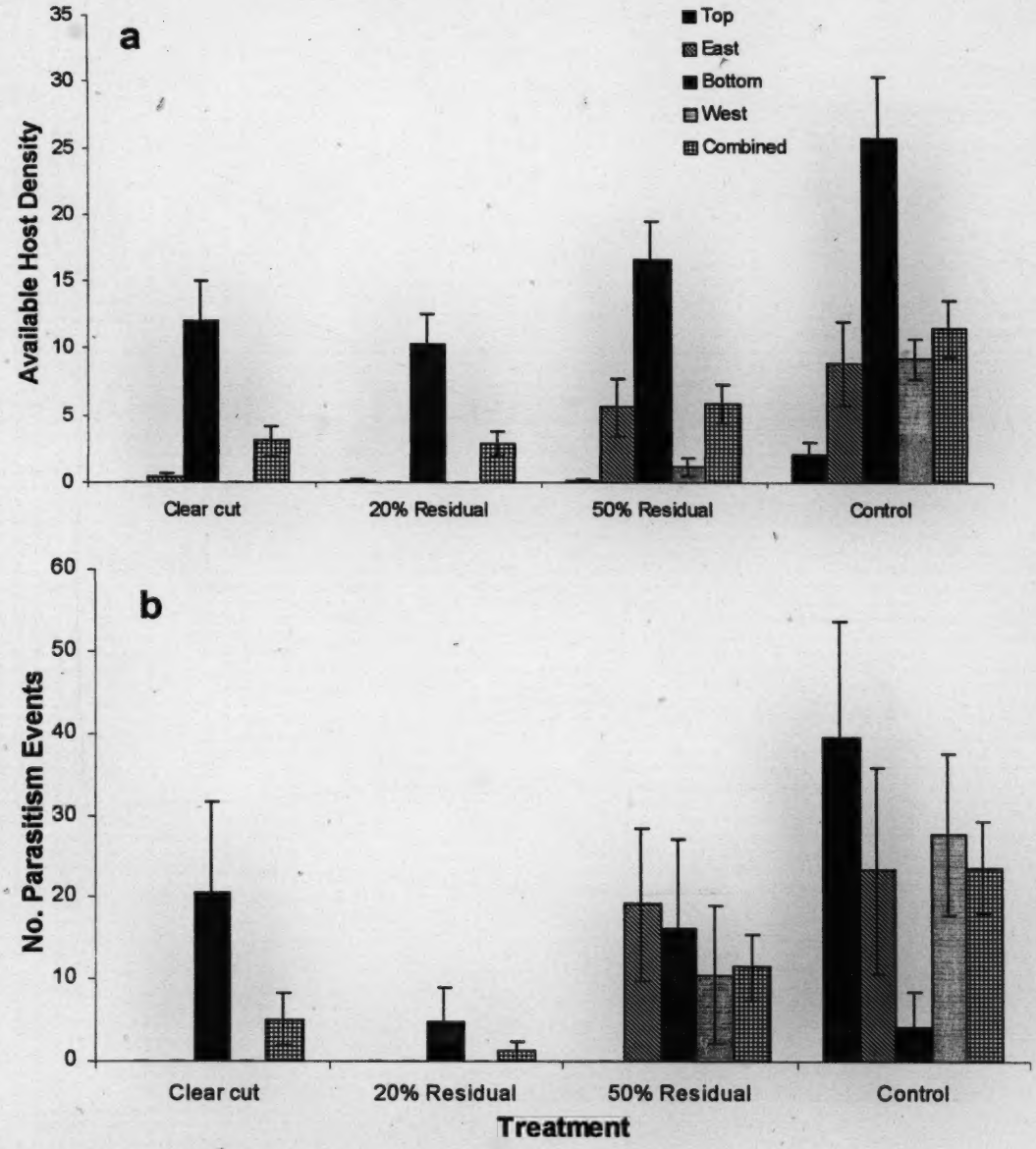

Figure 3.1. Comparisons of means (± SE) density (per 100 cm^2) of: a) available hosts and; b) number of parasitised available hosts for each treatment and log surface. Data represent all 144 bark samples collected on August 17, 1999.

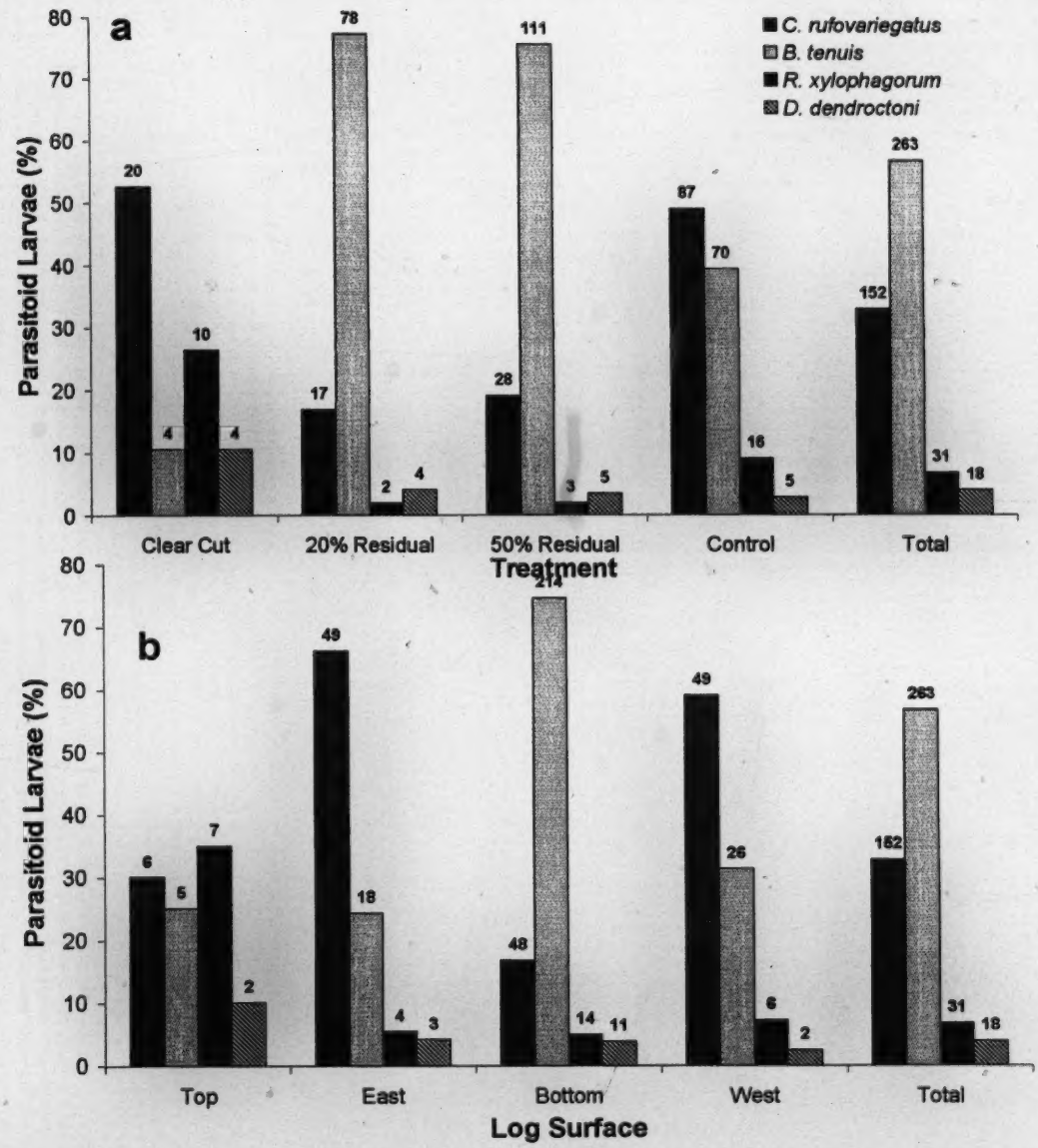

Figure 3.2. Percent of parasitoid larvae in samples collected from July 19, 1999 to July 21, 2000 represented by different species, partitioned by: a) harvesting treatment; and b) log surface. Number of parasitoid individuals is indicated at the top of each bar.

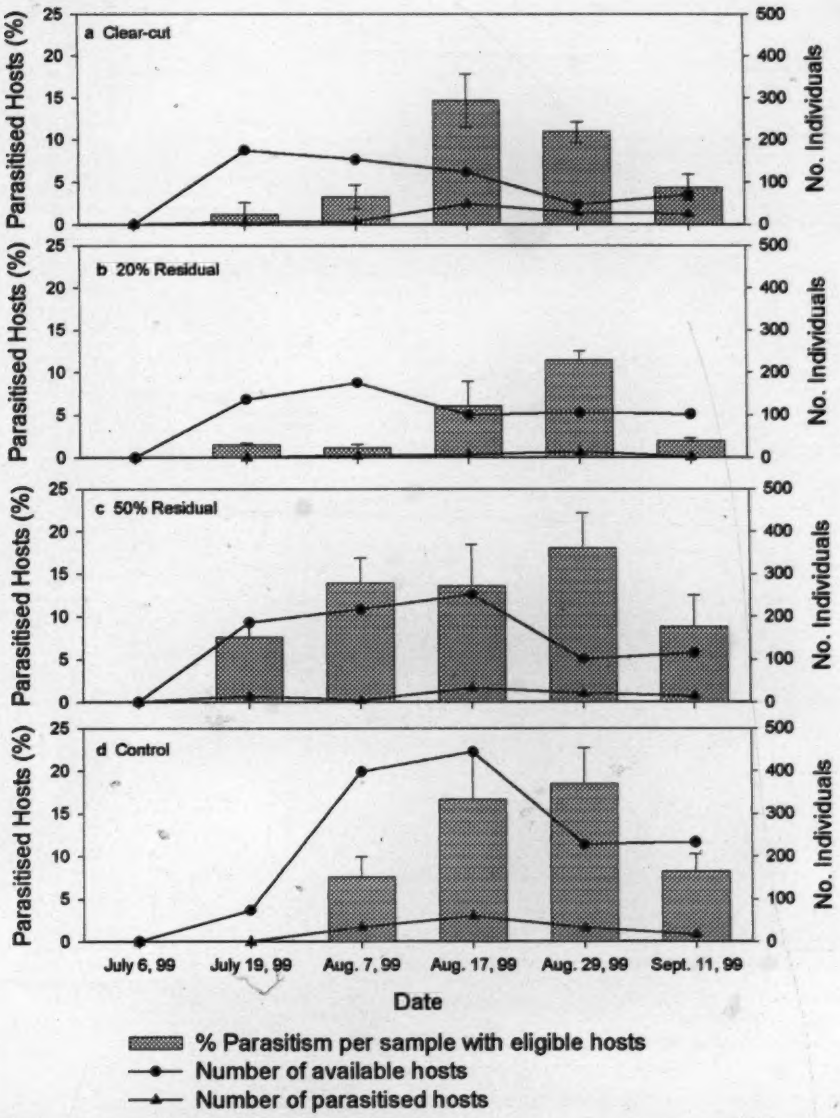

Figure. 3.3. Comparisons of means (± SE) % parasitism per sample containing available beetle hosts, total number of parasitised hosts, and total of available hosts for a) clear-cut, b) 20% residual, c) 50% residual, and d) control compartments.

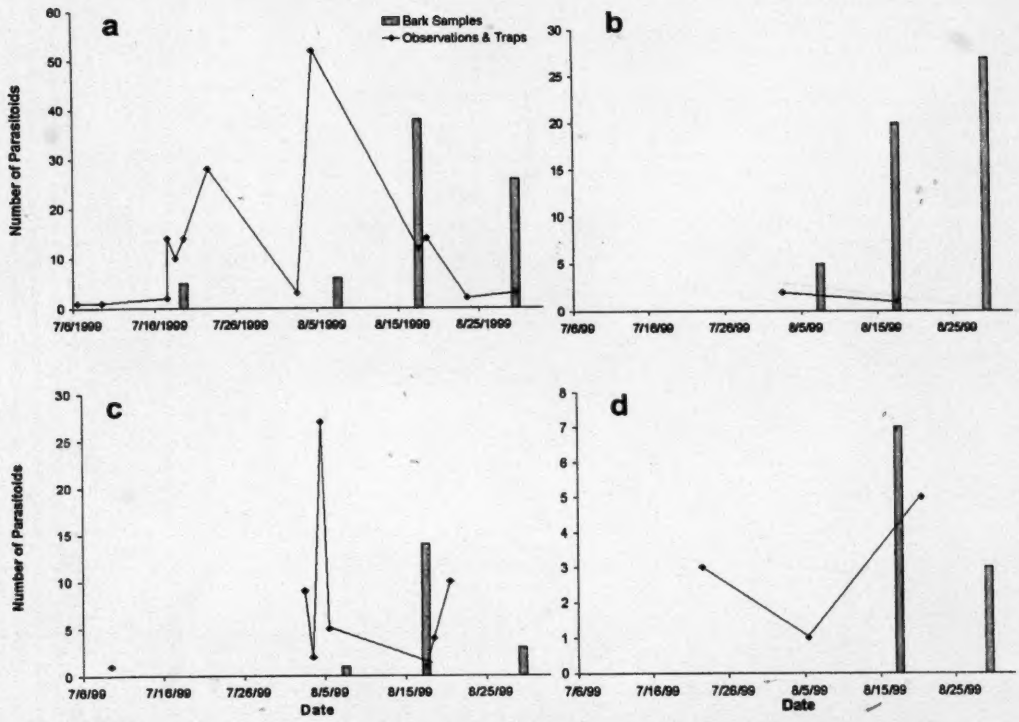

Fig. 3.4. Flight activities for parasitoids based on combined observations of specimens on logs and in Lindgren funnel, emergence and sticky traps and number of parasitoids present in 144 bark samples for each date (all treatment and log surfaces combined) for a) *Coeloides rufovariegatus*, b) *Bracon tenuis*, c) *Roptrocerus rufovariegatus*, and d) *Dinotiscus dendroctoni*.

Chapter 4

THESIS CONCLUSIONS

4.1 LEPIDOPTERAN PARASITISM

Collection of larval lepidopteran defoliators on aspen and spruce and their parasitoids resulted in a host-parasitoid list for Northwestern Alberta. This is by no means complete, but it does provide solid information to fill the void of information presently available on this topic. Although such information is required for a full understanding of forest trophic relationships and natural biological control in the boreal mixedwood, it is not readily available for any forest area in Canada. Most studies of host-parasitoid relationships are focused on single lepidopteran species and the associated parasitoid web (Dahlsten *et al.* 1977, Parry 1995, Turgeon 1994) and relatively few studies have sampled an entire community of canopy-dwelling Lepidoptera for their parasitoids (Hawkins and Lawton 1987, Memmott *et al.* 1994). Whole community information is required to fully address the impacts of anthropogenic disturbances on biodiversity.

Lepidoptera and their associated parasitoid communities were assessed for abundance, species richness and rate of parasitism. Overall, aspen in deciduous-dominated (DD) stands had higher lepidopteran and parasitoid

species abundance and richness compared to white spruce in conifer-dominated (CD) stands. In contrast, lepidopteran and parasitoid diversity and rate of lepidopteran parasitism was higher in CD stands than in DD stands. Morneau (2002) also noted that lepidopteran larvae diversity and abundance were lower in CD stands. Perhaps DD canopies provide warmer microhabitats for defoliators than CD canopies because they receive more solar radiation, and larvae (both defoliators and parasitoids), which are poikilothermic, doubtlessly benefit from warm temperature by assimilating their food more efficiently. A study of birds at EMEND suggested that relative abundance of foliage-gleaners was slightly greater in spruce stands (P=0.018) (Harrison, 2002) and this could further contribute to the differences observed by reducing defoliator and parasitoid abundance in spruce stands. Therefore, differences in stand composition, structure and biota are consistent with differences found between cover types for lepidopterans and their parasitoids.

Even though parasitoids are less abundant and less species rich in CD stands, it appears that they are able to parasitise a greater proportion of Lepidoptera than their DD counterparts (Chapter 2). Each parasitoid species in a complex contributes to maintaining low host population levels for a host species. For example, Parry (1997) noted that *Aleoides malacosomatos* (Mason) was an effective parasitoid of *Malacosoma disstria* larvae while *Itoplectis conquisitor* (Say) targeted pupae. A large and diverse complex of parasitoids is more apt to maintain a low population level of hosts as they target

vulnerable host stages. The parasitoid complex for major lepidopteran defoliators plays an important role in reducing the risk of outbreak of their host populations (Cerezke 1992, Harmsen and Rose 1983, Turchin and Taylor 1992, Vasic 1971).

Variable retention harvesting had little effect on lepidopteran parasitoid communities the first season post harvest. Although it was not statistically significant, there was a trend for lower parasitoid abundance in 50% and 20% residual compartments compared to control locations for CD and DD stands (Chapter 2). However, rates of parasitism observed among the Lepidoptera were not affected (Chapter 2). Lewis and Whitfield (1999) found that with disturbance braconid abundance did not change from that in the control forest but braconid species richness was higher in disturbed sites. Also, as sites were increasingly disturbed the species compliment changed more from control sites (Lewis and Whitfield 1999). This evidence suggests that future work may need to focus on species richness rather than abundance measures to accurately depict effects on parasitoid communities post harvest.

4.2 *DENDROCTONUS RUFIPENNIS* PARASITISM

In general, parasitic wasps are poorly known both biologically (Askew and Shaw 1986, Memmott *et al.* 1994) and taxonomically (LaSalle and Gauld 1992, 1993). In order to remedy this situation for the parasitoids of spruce beetle, which can be a significant pest of northern spruce stands, I conducted

baseline biological research to assess the parasitoid complex associated with *D. rufipennis* larvae. A novel medium was developed (Appendix 1) to rear the parasitoid larvae to adulthood, thereby facilitating species identification. A key to species and detailed drawings for mandibular sclerotization patterns was constructed (Appendix 2) to aid in future identification of parasitoid species using spruce beetle.

I found four parasitoid species using *D. rufipennis* and two of these, the braconids *Coeloides rufovariegatus* and *Bracon tenuis,* caused significant mortality. Interestingly, the chalcid *Roptrocerus xylophagorum*, *C. rufovariegatus* and *B. tenuis* were most abundant on the top, sides and bottom of the log surface, respectively. The fourth parasitoid, a chalcid, *Dinotiscus rufipennis*, was not abundant enough to establish the location they commonly parasitised hosts. Parasitoid lifestyles and host parasitoid species richness are important factors in understanding how parasitoid communities are affected by environmental changes (Mills 1994). Therefore, establishing the *D. rufipennis* parasitoid complex was the first step in establishing how the community may be affected by variable retention harvesting.

There was evidence that parasitoid attacks were concentrated at different locations on the infested bolt according to harvesting treatment. In control compartments, parasitoids commonly utilized the top of bolts but as the level of tree retention decreased, parasitoids increasingly attacked larvae at the bottom of the bolt (Chapter 3). Thus, the beneficial impact of these parasitoids

in resisting *D. rufipennis* population increase would be minimized in low tree retention harvesting as locations higher on the bolt may provide a refuge against parasitism. Elevated populations of *D. rufipennis* can enter stands surrounding harvested sites and kill healthy trees (Humphreys and Safranyik 1993, Schmid and Frye 1977, Werner *et al.* 1977) so it is important to conserve parasitoids that maintain low populations of *D. rufipennis*.

Host density is thought to be an important factor governing parasitism rates and such density-dependence is said to contribute to stability in host-parasitoid relationships (Brown and Cameron 1979, Morrison *et al.* 1980, Morrison and Strong 1981). Since many parasitoids have a regulatory effect on their hosts (Hassell 1986; LaSalle 1993; LaSalle and Gauld 1993), increases in parasitism as host populations grow are held to be crucial to minimize insect outbreaks (Bouletreau 1986). Interestingly, host density did not affect parasitism rates for lepidopteran hosts observed in my study (Chapter 2) and samples containing a higher density of *D. rufipennis* larvae actually had lower parasitism (Chapter 3).

4.3 FUTURE DIRECTIONS

I believe that parasitoids need to be studied intensively to get an accurate understanding of the factors influencing host-parasitoid interactions in biological communities. For example, my rarefaction curves for lepidopteran

parasitoids suggest that parasitoid diversity was not sampled well enough to get an accurate estimation of parasitoid species in the community (Chapter 2). Over 54% of parasitoid species identified were only collected once, 82% of parasitoid species were collected fewer than 5 times (all lepidopteran hosts combined). Within a host-parasitoid assemblage there is a complex web of interactions involving many parasitoids with a few of these interactions dominating the system (Memmott and Godfray 1993). Thus, rarer parasitoid species that play a lesser role in the assemblage require greater sampling effort for collection than in this study.

In addition to profiting from increased sampling effort, any biodiversity study would benefit from examination of data about other faunal elements. I focused exclusively on hymenopterous parasitoids and their relationships with their specific hosts. In the literature it has been shown that parasitoid abundance has a delayed response to changes in host abundance (LaSalle and Gauld 1993, Parry *et al.* 1997, 1998, Waage and Greathead 1986) so host-parasitoid complexes may react slowly to harvesting treatment. Thus, it would be important to collect host and parasitoids in years following harvest treatment to note the full effect of the harvesting treatment. Understanding the significance of changing host-parasitoid relationships requires simultaneous studies of the response of other organisms to the changes.

The most important contribution of my thesis is with respect to establishing host-parasitoid relationships and describing unknown aspects of

parasitoid biology. This basic biological information was the backbone for all my comparisons and provides much fuel for future studies. Further work can be aimed at the following questions. What additional parasitoid species do we have in Northwestern Alberta? What are the parasitoid and host relationships? What role do parasitoids play in the ecology of the forest canopy or in coarse woody material? Do all parasitoids respond to host density or harvesting treatments and what are the likely effects of widespread industrial forestry on these relationships?

Overall, my thesis used a variety of sampling and analytical techniques to better understand host-parasitoid associations and the factors that influence these relationships in light of variable retention harvesting in Northwestern Alberta. Important biological information was gathered about little known species of Hymenoptera, defoliating Lepidoptera and *D. rufipennis* larvae that will support future studies aimed at specific management questions or provide the basis for a full inventory of these taxa in the northern mixedwood. Host-parasitoid relationships have been shown to be responsive to location, host density, cover type and harvesting treatment and knowledge of these relationships contributes to a better overall understanding of the complex ecosystem that comprises the northern mixedwood forest.

4.4 REFERENCES

Askew, R.R. and M.R. Shaw. 1986. Parasitoid communities: their size, structure, and development. *In:* Insect Parasitoids. (K. Waage and D. Greathead, Eds.), pp. 225-264. Academic Press, London.

Bouletreau, M. 1986. The genetic and co- evolutionary interactions between parasitoids and their hosts. *In*: Insect parasitoids (Waage, J. and D. Greathead, Eds.), Academic Press, London, pp. 169-200.

Brown, M.W. and E.A. Cameron. 1979. Effects of disparlure and egg mass size on parasitism by the gypsy moth egg parasite, *Ooencyrtus kuwanai*. *Env. Entomol.* **8**: 77-80.

Cerezke, H.F. 1992. Large aspen tortix. Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta. For. Leafl. 21.

Dahlsten, D.L., R.F. Luck, E.I. Schlinger, J.M. Wenz, and W.A. Copper. 1977. Parasitoids and predators of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae), in low to moderate populations in central California. *Can. Entomol.* **109**: 727-746.

Harmsen R. and M.R. Rose. 1983. Habitat effects on larval mortality in the forest tent caterpillar, Malacosoma disstria (Lepidoptera: Lasiocampidae). Proceedings of the Entomological Society of Ontario, **114**, 87-89.

Harrison, R.B. 2002. Stand-level response of boreal forest songbirds to experimental partial-cut harvest in Northwestern Alberta. Thesis.

Hassell, M.P. 1986. Parasitoids and population regulation. *In*: Insect Parasitoids (Waage, J. and D. Greathead, Eds.), Academic Press, London, pp. 201-224.

Hawkins, B.A. and J.H. Lawton. 1987. Species richness for parasitoids of British polyphagous insects. *Nature* **326**, 788-790.

Humphreys, N. and L. Safranyik. 1993. Spruce Beetle. Canada- B.C. Partnership Agreement FRDA II: For. Pest Leaf. 13. 7pp.

LaSalle J. and I.D. Gauld. 1992. Parasitic Hymenoptera and the biodiversity crisis. *Redia* **74**: 315- 334.

LaSalle, J. 1993. Parasitic Hymenoptera, Biological Control and Biodiversity. *In*: Hymenoptera and Biodiversity (LaSalle, J. and I.D. Gauld, Eds.), CAB International, Wallingford, pp. 197-215.

LaSalle, J. and I.D. Gauld. 1993. Hymenoptera: Their Diversity and Their Impact on the Diversity of Other Organisms. *In*: Hymenoptera and Biodiversity (LaSalle, J., and I.D. Gauld, Eds.), CAB International, Wallingford, pp. 1-26.

Lewis, C.N. and J.B. Whitfield. 1999. Braconid wasp (Hymenoptera: Braconidae) diversity in forest plots under different silvicultural methods. *Community and Ecosystem Ecol.* **28** (6): 986- 993.

Memmott, J. and H.C.G. Godfray. 1993. Parasitoid webs. *In*: Hymenoptera and Biodiversity (LaSalle, J. and I.D. Gauld, eds.), CAB International, Wallingford, pp. 217- 234.

Memmott, J., H.C.J. Godfray and I. D. Gauld. 1994. The structure of a tropical host- parasitoid community. *J. Anim. Ecol.* **63**: 521- 540.

Mills, N.J. 1994. Parasitoid guilds: defining the structure of the parasitoid communities of endopterygote insect hosts. *Env. Entomol.* **23(5)**: 1066-1083.

Morneau, L. 2002. Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest of Alberta. Thesis.

Morrison, G., W.J. Lewis and D.A. Nordlund. 1980. Spatial differences in *Heliothis zea* egg density and the intensity of parasitism by *Trichogramma* spp.: an experimental analysis. *Env. Entomol.* **9**: 149-152.

Morrison, G. and D.R. Strong. 1981. Spatial variation in egg density and the intensity of parasitism in a neotropic chrysomelid (*Cephaloleia consanguinea*). *Ecol. Entomol.* **6**: 55-61.

Parry D. 1995. Larval and pupal parasitism of the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), in Alberta, Canada. *Can. Entomol.* **127**: 877-893.

Parry, D., J.R. Spence and W.J.A. Volney. 1997. Responses of natural enemies to experimentally increased populations of the forest tent caterpillar, *Malacosoma disstria*. *Ecol. Entomol.* **22**: 97-108.

Parry, D., J.R. Spence and W.J.A. Volney. 1998. Budbreak phenology and natural enemies survival of first-instar forest tent caterpillar (Lepidoptera: Lasiocampidae). *Env. Entomol.* **27(6)**: 1368-1374.

Schmid, J.M. and R.H. Frye. 1977. Spruce beetle in the Rockies. USDA Forest Service, Rocky Mountain Forest and Range Experimental Station. *Gen. Tech. Rept.* RM-49, 38 pp.

Shapiro, B.A. and J. Pickering. 2000. Rainfall and parasitic wasp (Hymenoptera: Ichneumonidae) activity in successional forest stages at Barro Colorado Nature Monument, Panama and La Selva Biological Station, Costa Rica. *Agric. For. Entomol.* **2:** 39-47.

Turgeon, J.J. 1994. Status of research on the development of management tactics and strategies for the spruce bud moth in white spruce plantations. *For. Chron.* **68(5)**: 614-622.

Turchin P. and A.M. Taylor. 1992. Complex dynamics in ecological time series. *Ecology*. **73**: 289-305.

Vasic, K. 1971. A biological method of control of *Lymantria dispar* L. and *Diprion pini* L. Institute of Forestry and Wood Industry of Servia, Belgrade, Yugoslavia. 134pp.

Waage, J. and D. Greathead. 1986. Preface. *In*: Insect parasitoids (Waage, J. and D. Greathead, Eds.), Academic Press, London, pp. xi-xii.

Werner, R.A., B.H. Baker and P.A. Push. 1977. The spruce beetle in white spruce forests of Alaska. U.S.D.A For. Serv. Gen. Tech. Rept. PNW-61. 13pp.

Appendix 1

RECIPE FOR REARING MEDIUM FOR PARASITOIDS OF *PICEA GLAUCA* BUD DEFOLIATORS AND *DENDROCTONUS RUFIPENNIS*.

Ingredients:

500 mL Distilled water

20 g Cornmeal

15g Agar

3.3 g Aromycin (bactericide)

0.3 mL Formalin

5 mL BDP stock solution (fungicide) containing: 50 mg Phenol

16 mg Benomyl

10 mg Botran

5 mL 50% Ethanol

1. Place distilled water, cornmeal and agar in 1 liter Erlenmeyer flask. Add stir bar to mixture and place loose foil cover over mouth of flask.
2. Set flask in autoclave and set the program for 20 minutes on the liquid cycle.
3. After autoclave session finished, place flask on stir plate. Turn on the stir plate so liquid slowly mixes.

4. When solution cools to touch (less than 40^0C), add the aromycin, formalin and BDP stock solution. Allow mixture to blend thoroughly.
5. Pour 3-4 mL of solution into the bottom of small containers (approximately 10 mL).
6. Allow media to cool and gel in containers before nesting containers.
7. If medium is not to be used immediately, containers can be stacked, sealed in plastic bags and frozen to maintain freshness.

Appendix 2

CEPHALIC MORPHOLOGY OF LARVAE OF PARASITOIDS OF THE SPRUCE BEETLE AND A KEY TO SPECIES.

2.1 INTRODUCTION

Parasitic Hymenoptera are relatively poorly known taxonomically and a large proportion of taxa remains to be described (LaSalle and Gauld 1992). Although keys to genera of adults of most families are available and generally current, keys to species exist for very few genera in Canada. The situation is far worse for larvae; very few larvae have been described and keys are non-existent. This poses challenges for studies of parasitoid biology and parasitism as the parasitoid assemblages of a single host species usually consist of at least a few species which co-occur in time and space, thereby making it crucial to be able to discriminate accurately among immature stages of different species. To obtain positive identification parasitoids may be reared to adulthood using an agar-based medium (Appendix 1); however, the success rate is sometimes low for unknown reasons. Therefore, the constructions of keys of larvae associated with specific hosts provide a valuable tool which can aid in elucidation of parasitoid behavior and assessment of impacts on the host population. Most of the sclerotized structures in Hymenoptera larvae are

concentrated in the cephalic region and this area is a good source of useful taxonomic characters. Through extensive rearing of larvae and association of larval exuvia with adults I have been able to describe the cephalic structures of four species of parasitoids associated with the spruce beetle, *Dendroctonus rufipennis* (Kirby), in northwestern Alberta, and construct a key to species.

2.2 METHODS

To identify unsuccessfully reared parasitoid larvae, known larval exuvia from reared parasitoid adults were examined to establish distinguishing mandibular characteristics for each larval parasitoid species. Known exuvia were removed from the cocoon and rehydrated in water for 4-8 hours. Rehydrated larval exuvia were placed in 10% KOH solution on a warming plate for 1-3 hours to clear remaining tissue from exuvia, length of clearing time was longer for larger parasitoid larvae. Cleared larvae were placed in glycerin on a well slide and examined with light transmission microscopy. Once distinguishing characteristics for each species were established, unsuccessfully reared parasitoid larvae were cleared and identified using the same procedure. Larval exuvia were removed from deceased Hymenopteran pupae within cocoons for identification using the same procedure. Identified larvae were placed into minute Lepidoptera genitalia vials with glycerin for storage.

Methods for extracting exuvia, clearing and examining larvae were modified from procedures established by Finlayson (1960).

Digital photographs of head capsules were taken through a microscope. Multiple photographs of each species, from several angles, were combined to fully illustrate differences among species. These images were converted into composite line drawings in CorelDRAW 10 (Corel Corporation 2000). Structure identification was based from Capek (1970) and Finlayson (1960).

2.3 RESULTS

Four hymenopteran parasitoids of *D. rufipennis* were identified from unsuccessfully reared pupal exuvia and dead larval skins (Fig.1). The two most common parasitoids identified were *Coeloides rufovariegatus* (Provancher) (Fig. 2) and *Bracon tenuis* Muesebeck & Walley (Hymenoptera: Braconidae) (Fig. 3). These species had similar facial sclerotization but *C. rufovariegatus* were distinguished from *B. tenuis* by a more dorso- ventrally elongated labial sclerite, hypostomal spurs which did not touch the stipial sclerite or hypostoma, and a heavily sclerotized mandibular tooth. The two chalcid parasitoids, *Roptrocerus xylophagorum* (Ratzeburg) (Chalcidoidea: Pteromalidae) (Fig. 4) and *Dinotiscus dendroctoni* (Ashmead) (Chalcidoidea: Pteromalidae) (Fig. 5), had negligible facial sclerotization. Thus, only mandibular characteristics were used to distinguish species. *R. xylophagorum* had mandibles with a short, stout blade

relative to the mandible length while *D. dendroctoni* possessed a hooked mandible blade that was slender and elongate relative to the mandible length.

2.4 PARASITOID DESCRIPTION

Coeloides rufovariegatus

C. rufovariegatus had well developed facial and mandibular sclerotization with lightly sclerotized antennae. The larvae possess an elongate labial sclerite with hypostomal spurs that do not touch the stipial sclerite or hypostoma, a well developed epistoma, an easily visible silk press, and a mandible with very heavy sclerotization comprised of one main tooth and many lesser teeth.

The flight window for *C. rufovariegatus* adults was from June 6 to September 11, 1999. This parasitoid was most commonly associated with fourth instar *D. rufipennis* larvae (75%) located on the lower portions of the bolt surface in clear cut and control compartments. *C. rufovariegatus* parasitised the most beetle larvae (49%) compared with the other identified parasitoids and one parasitoid larvae developed per beetle larva (Chapter 3).

Bracon tenuis

B. tenuis larvae had well developed facial and mandibular sclerotization. Larvae had a less elongate labial sclerite when compared to *C. rufovariegatus* larvae, hypostomal spurs did not touch the stipial sclerite or hypostoma, and the mandible was heavily sclerotized with one tooth.

A few *B. tenuis* adults were observed during early August 1999. Parasitoid larvae most commonly parasitised fourth instar *D. rufipennis* larvae (81%) located on the bottom of the log surface in 20% and 50% residual compartments. *B. tenuis* larvae parasitised (37%) of beetle larvae and an average of 9 parasitoid larvae developed per beetle larva (Chapter 3).

Roptrocerus xylophagorum

R. xylophagorum larvae did not have well developed facial and mandibular sclerotization. Larvae had lightly sclerotized mandibles to allow for distinguishing characteristics. The mandibles had a blade shorter than the length of the mandible base with one tooth.

Adult R. xylophagorum were observed in flight near beetle infested bolts during August 3 through 21, 1999. Parasitoid larvae most commonly parasitised fourth *instar D. rufipennis* larvae (78%) in higher proportions on the top of the log surface in clear cut compartments. *R. xylophagorum* larvae parasitised (10%) of beetle larvae and 1 parasitoid larvae developed per beetle larva (Chapter 3).

Dinotiscus dendroctoni

D. dendroctoni larvae did not have well developed facial and mandibular sclerotization. Larvae had lightly sclerotized and the mandibles had a blade longer than the length of the mandible base with one tooth with a hooked tip.

Adult parasitoids were noted in flight during July 20 to August 21, 1999. Parasitoid larvae were reared in low numbers but were only reared from fourth instar *D. rufipennis* larvae found in slightly higher proportions on the top of bolts in clear cut compartments. *D. dendroctoni* larvae parasitised (5%) of beetle larvae and 1 parasitoid larvae developed per beetle larva (Chapter 3).

2.5 REFERENCES

Capek, M. 1970. A new classification of the Braconidae (Hymenoptera) based on the cephalic structures of the final instar larva and biological evidence. *Can. Entomol.* **102:** 846- 875.

CorelDRAW Version - 10.0. 2000. Corel Corporation and Corel Corporation Limited.

Finlayson, T. 1960. Taxonomy of cocoons and puparia, and their contents, of Canadian parasites of *Neodiprion sertifer* (Geoff.) (Hymenoptera: Diprionidae). *Can. Entomol.* **92:** 21- 47.

LaSalle, J., I.D. Gauld. 1992. Hymenoptera: Their diversity, and their impact on the diversity of other organisms. *In*: Hymenoptera and Biodiversity (LaSalle, J. and I.D. Gauld, eds.), CAB International, Wallingford, pp. 1- 26.

Figure 1. Key to the four parasitoid larvae reared in association with *D. rufipennis* larvae.

1.a. Head capsule with well developed mandibular sclerotization (Ichneumonoidea: Braconidae) 2

b. Head capsule without well developed mandibular sclerotization (Chalcidoidea: Pteromaildae) 3

2.a. Hypostomal spurs not touching stipial sclerite and hypostoma, well developed epistoma, heavily sclerotized mandible with multiple teeth, possess a more dorso-ventrally elongate labial sclerite (Fig.1) .....

C. rufovariegatus (Provancher)

b. Hypostomal spurs touching stipial sclerite and/or hypostoma, mandibular tooth not heavily sclerotized, antennae present and lightly sclerotized, labial sclerite is less dorso-ventrally elongate (Fig.2) .....

B. tenuis Muesebeck & Walley

3.a. Mandibles with a short stout blade relative to mandible length (Fig. 3).....

R. xylophagorum (Ratzburg)

b. Mandible blade long and slender relative to mandible length, mandible blade with a hooked tip (Fig. 4)..... ***D. dendroctoni*** (Ashmead)

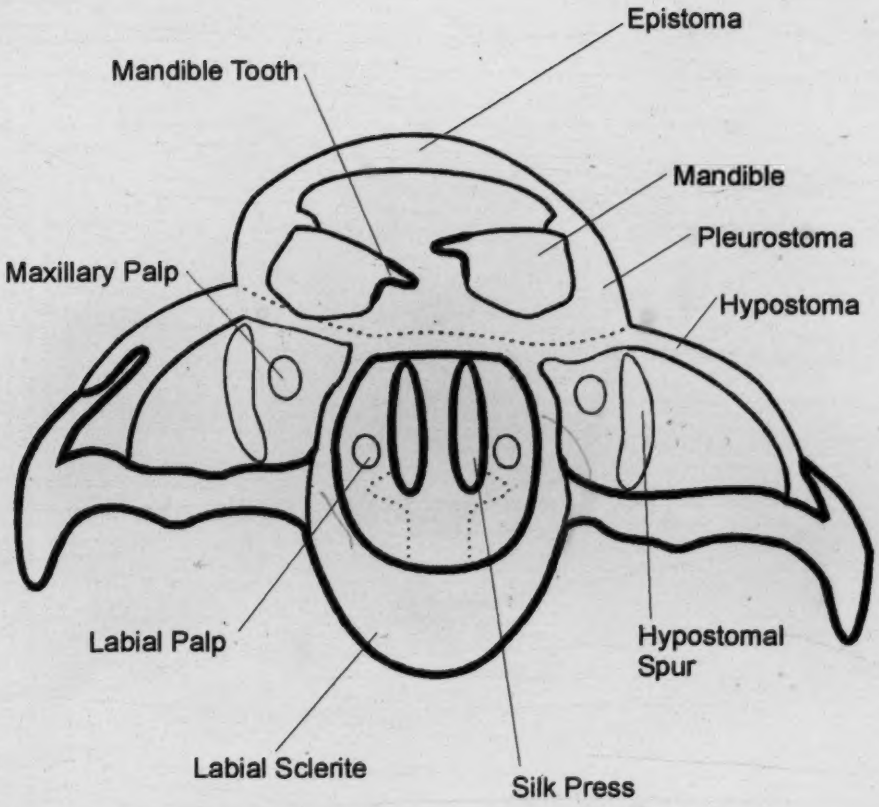

Figure 2. Composite drawing of final instar *Coeloides rufovariegatus* (Prov.) (Hymenoptera: Braconidae: Braconinae) cephalic features.

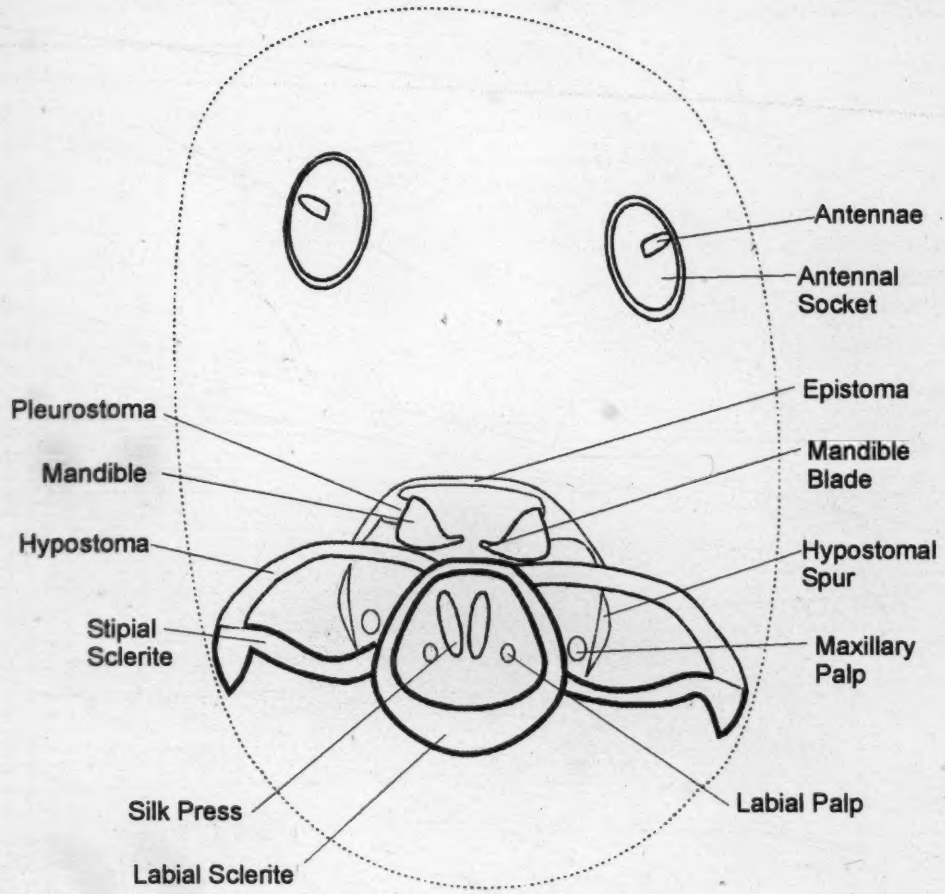

Figure 3. Composite drawing of final instar *Bracon tenuis* Mues. & Wall. (Hymenoptera: Braconidae: Braconinae) cephalic features.

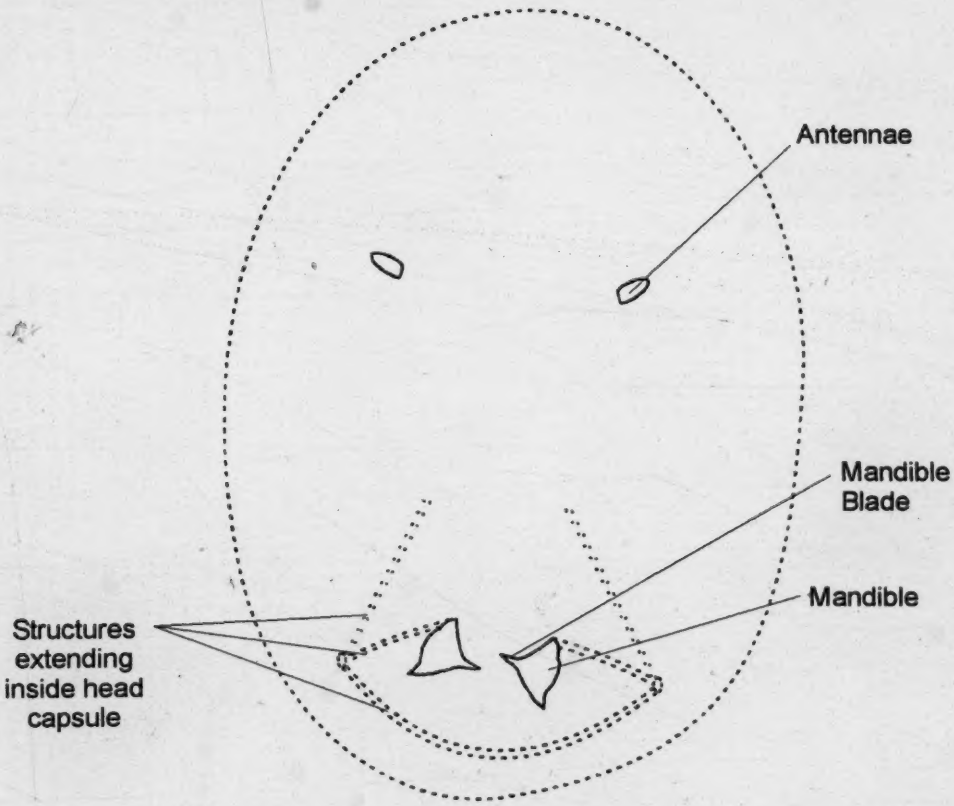

Figure 4. Composite drawing of final instar *Roptrocerus xylophagorum* (Ratz.) (Hymenoptera: Chalcidoidea: Pteromalidae) cephalic features.

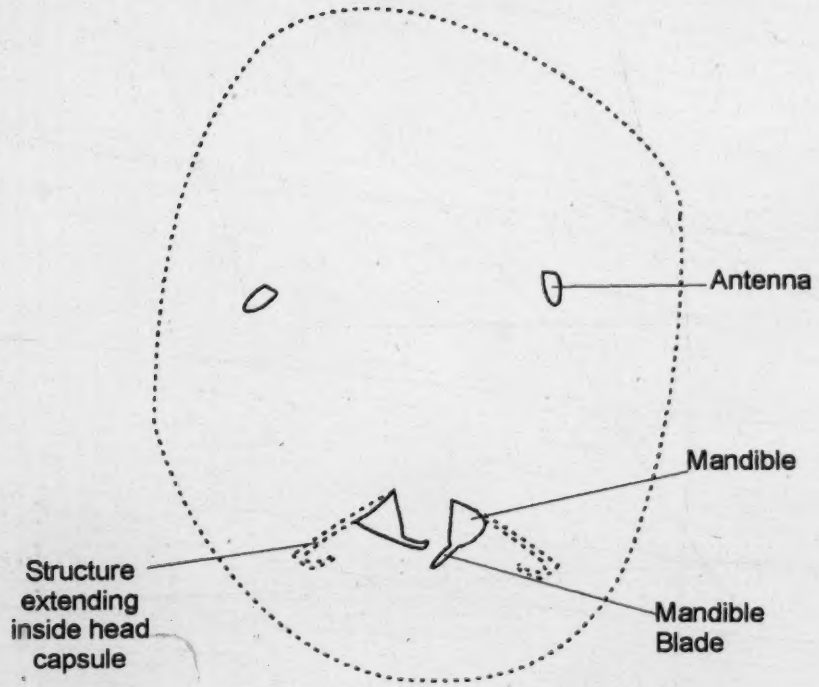

Figure 5. Composite drawing of final instar *Dinotiscus dendroctoni* (Ash.) (Hymenoptera: Chalcidoidea: Pteromalidae) cephalic features.